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# 1.—Spilitic pillow lavas at Mt. Hunt, Western Australia

by J. A. Hallberg\*

*Manuscript received 27 July; accepted 21st September 1971*

## Abstract

Spilitic pillow lavas form irregular zones within a sequence of unpillowed high-Mg basalts near Mt. Hunt, Western Australia. These pillows are strongly zoned, alkali-enriched and are petrologically and chemically distinct from the tholeiitic basalts which dominate Archaean volcanic belts throughout the Eastern Goldfields region. It is suggested that the spilitic pillows were derived from lavas similar in composition to the high-Mg basalts of the Mt. Hunt sequence.

## Introduction

Mt. Hunt is 19 km south of Kalgoorlie, to the east of the Kalgoorlie-Kambalda road. Williams (1970) has established the Mt. Hunt sequence as the type area for the Mulgabbie Formation. He suggests a correlation of the Mt. Hunt sequence with a volcanic belt passing through the Corsair, Golden Ridge and Duplex Hill districts. The structure of the area is complex and interpretation is hampered by poor outcrop in critical areas. Essentially, the sequence consists of several belts of NNW-trending, west-facing basalt with intercalated bands of contorted jaspilite. A thick, conformable, west-facing layered sill and several semi-conformable masses of serpentized ultramafic have been intruded along sedimentary horizons. Discordant porphyry dykes are common and the sequence has been highly folded and faulted, and in places subjected to deep weathering and lateritization.

The massive basalt flows forming the bulk of the sequence are magnesium in nature (8% to 15% MgO) and show the various "quench" textures and skeletal crystal forms which typify this group of basalts throughout the Eastern Goldfields region. Within the stratigraphically older high-Mg basalt flows to the east of Mt. Hunt are several highly altered variolitic horizons and patchy zones where pillows are developed. The best exposure of these pillow lavas is in a small creek bed, 450 m due east of the Mt. Hunt trig point (Figure 1). The pillows range from 0.5 m to 2.5 m in length, and are moderately flattened in the plane of bedding. They are concentrically zoned with mottled greenish cores showing irregular fractures and variolitic margins with closely spaced joints perpendicular to the pillow outline. Dense chilled skins up to 5 cm in thickness surround the pillows. The matrix in which the pillows are set appears to have been a peperite of glassy pillow fragments with some sedimentary material.

## Petrology

Chilled pillow skins are formed of a dense, felted, fine-grained mixture of chlorite, tremolite and clinozoisite. Variolitic pillow margins consist of numerous spherical varioles up to 1 cm in diameter set in a dusted mesostasis of chlorite, clinozoisite, albite and tremolite. The outlines of scattered pyroxene phenocrysts which have been replaced by uraltite can occasionally be seen. The varioles contain radiating sheaves of partially saussuritized plagioclase (An<sub>5</sub>) intergrown with elongate needles of uraltized pyroxene. A thin selvage of granular pyroxenes replaced by uraltite commonly surrounds the varioles. Pillow cores are filled with up to 65% ragged, randomly oriented lathes of plagioclase (An<sub>5-25</sub>) in a groundmass of chlorite, clinozoisite, tremolite and fine-grained opaques. The plagioclase lathes are water-clear and well twinned.

The mineralogy of these pillows differs markedly from that of tholeiitic pillows throughout the Eastern Goldfields, which are invariably composed of a pleochroic green amphibole and plagioclase with only trace amounts of chlorite, epidote, clinozoisite and quartz (Hallberg, 1971). The composition of the plagioclase in the pillows at Mt. Hunt is more sodic than that in the normal tholeiitic pillows, which contain either a primary labradorite or andesine or a metamorphic oligoclase. There is no indication that the pillows at Mt. Hunt have undergone recrystallization during low-grade regional metamorphism.

## Analytical Data

Fresh samples of the core, margin and matrix of a well-formed pillow in the creek bed exposure were subjected to major and trace element analysis (Table 1). Results indicate that the pillow becomes enriched in Si and Na and depleted in K, Rb, Mg and Fe towards its core; the entire pillow is enriched in volatiles. Ti, Al and most of the less mobile trace elements show little variation across the pillow. This zonation contrasts with the more uniform distribution shown by most tholeiitic pillows in the Eastern Goldfields (Hallberg, 1971). The Mt. Hunt pillow is also enriched in alkalis and volatiles with respect to the tholeiites as shown in Table 1. Perhaps the most unusual feature of the pillow is its high Cr and Ni contents which contrast with previously reported values for both tholeiites and spilites.

\* Division of Mineralogy, CSIRO, W.A. Laboratories, Floreat Park, W.A. 6014.

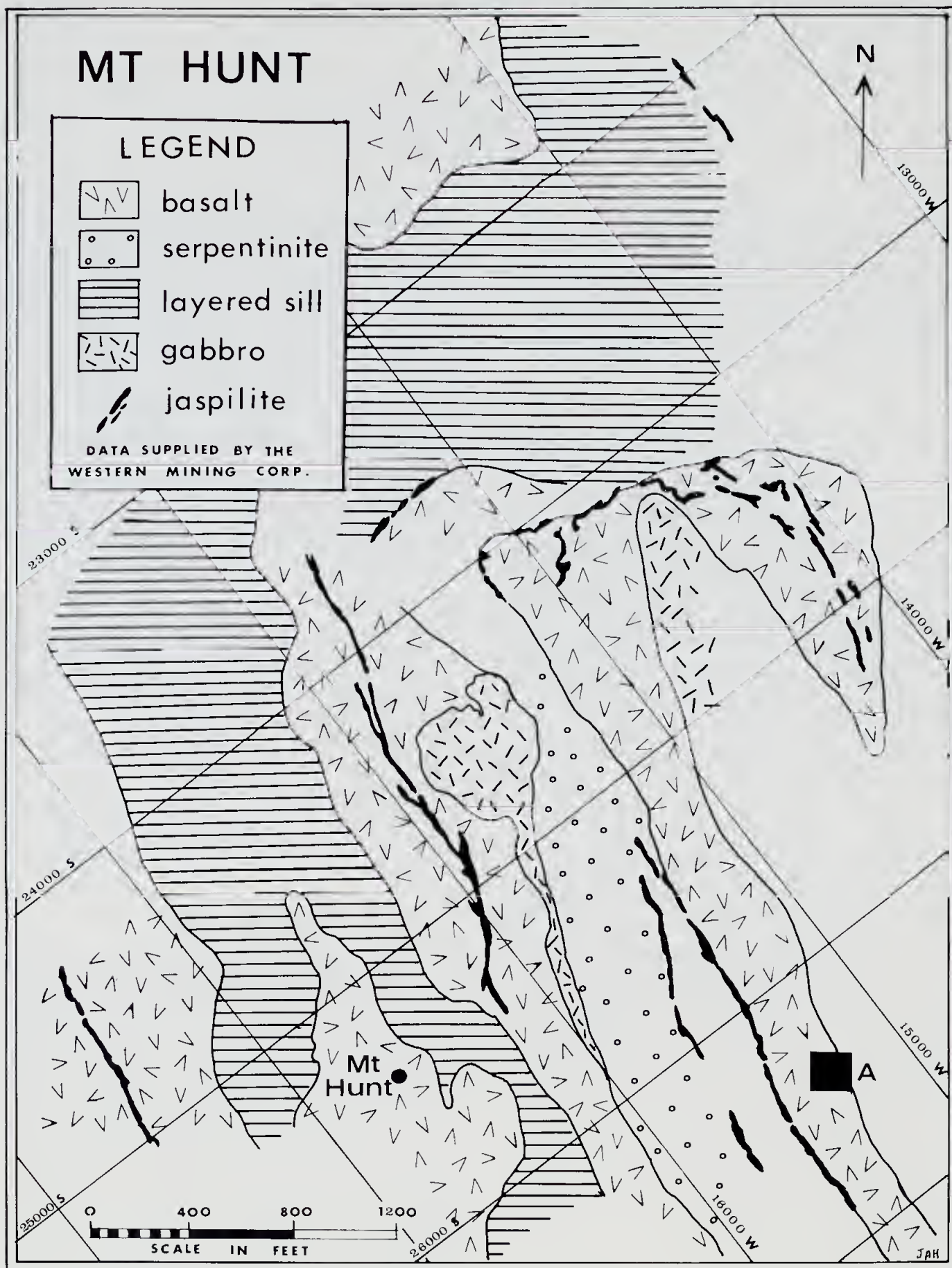


Figure 1.—Geological map of Mt. Hunt and vicinity. Area "A" is the creek-bed exposure of spilitic pillow lavas.



TABLE 1

Analysis of spilitic pillow lavas from Mt. Hunt

	1	2	3	4	5	6	7
SiO <sub>2</sub>	46.25	54.48	57.10	51.4	52.81	49.6	48.33
Al <sub>2</sub> O <sub>3</sub>	16.12	14.25	16.85	14.8	13.42	16.0	15.44
Fe <sub>2</sub> O <sub>3</sub>	2.51	2.29	2.48	1.5	2.27	3.8	
FeO	9.45	7.75	3.76	9.1	7.40	6.1	8.58*
MgO	9.96	8.07	4.35	6.7	9.81	5.1	7.41
CaO	7.63	6.99	6.77	10.7	9.12	6.6	8.02
Na <sub>2</sub> O	0.67	0.93	5.12	2.7	1.94	4.3	4.96
K <sub>2</sub> O	1.54	1.03	0.06	0.18	0.43	1.28	0.72
H <sub>2</sub> O <sup>+</sup>	3.72	2.98	1.92	1.0	1.79	3.4	
H <sub>2</sub> O <sup>-</sup>	0.41	0.19	0.69		0.25		
CO <sub>2</sub>	0.33	0.35	0.10	0.1	0.25	1.63	
TiO <sub>2</sub>	0.77	0.75	0.74	0.92	0.60	1.57	0.59
P <sub>2</sub> O <sub>5</sub>	0.11	0.08	0.08	0.13	0.12	0.26	
MnO	0.28	0.23	0.14	0.21	0.16	0.15	
Total	99.75	100.47	100.16				

Co	90	71	59	59	65
Cr	817	891	841	395	901
Cu	103	97	82	98	67
Ni	285	222	280	161	243
Rb	66	41	4	9	8
Sr	90	95	92	105	176
Y	37	33	22	22	17
Zn	176	138	99	112	71
Zr	68	66	67	60	71

Q	—	14.2	6.9	0.8	5.3
or	9.5	6.3	0.3	1.0	2.6
ab	5.9	8.1	44.5	23.5	16.4
an	38.1	32.8	23.4	28.0	27.3
di {wo	0.3	1.0	4.3	10.4	7.5
en	0.2	0.6	2.9	5.4	4.8
fs	0.1	0.3	1.0	4.6	2.2

hy {en	23.6	20.1	8.1	11.6	19.8
fs	13.8	11.6	2.9	9.9	9.1

ol {fo	1.5	—	—	—	—
fa	0.9	—	—	—	—

mt	3.8	3.4	3.7	2.2	3.2
il	1.5	1.4	1.4	1.7	1.1
ap	0.2	0.2	0.2	0.3	0.2

1 = matrix, spilitic pillow, Mt. Hunt, W.A.

2 = margin, spilitic pillow, Mt. Hunt, W.A.

3 = core, spilitic pillow, Mt. Hunt, W.A.

4 = average Eastern Goldfields tholeiitic basalt (Hallberg, 1971).

5 = average of five high-Mg basalts, Mt. Hunt, W.A.

6 = average spilite (Valance, 1960).

7 = average of 53 spilites, Virgin Islands (Hekinian, 1971).

CIPW norms calculated on a volatile-free basis.

\* Total Fe as FeO.

## Affinities

In morphology, mineralogy and chemistry the Mt. Hunt pillows are similar to reported spilites. Vallance (1960, p. 22) notes that "Variolitic textures are common in many spilites . . .", and that "Amygdules and veins appear in almost all recorded spilites but unfilled cavities, on the other hand, are rare". Bailey *et al.* (1964) describe similar pillows from the Franciscan Formation of California and Hekinian (1971), highly variolitic pillows from the U.S. Virgin Islands. Amstutz (1967) and Hekinian (1971) list albite, chlorite, epidote, calcite and iron oxides as the major constituents of volcanic spilites. Spilites may contain a calcic augite or salite. Vallance (1960) maintains that the only distinguishing chemical characteristic of spilites is their high volatile content. In this respect it should be noted that the volatile content of the Mt. Hunt pillow is much greater than that of the average Coolgardie-Norseman basalt (Table 1). Spilites also tend to be enriched in

alkalis (Amstutz, 1967). Chemically, the pillow from Mt. Hunt compares closely with spilite analyses reported by Vallance (1960) and Hekinian (1971), as shown in Table 1, and with pillows from the Franciscan Formation (Bailey *et al.*, 1964), as shown in Figure 2. On the basis of these similarities it is concluded that the pillowed units at Mt. Hunt represent true spilites.

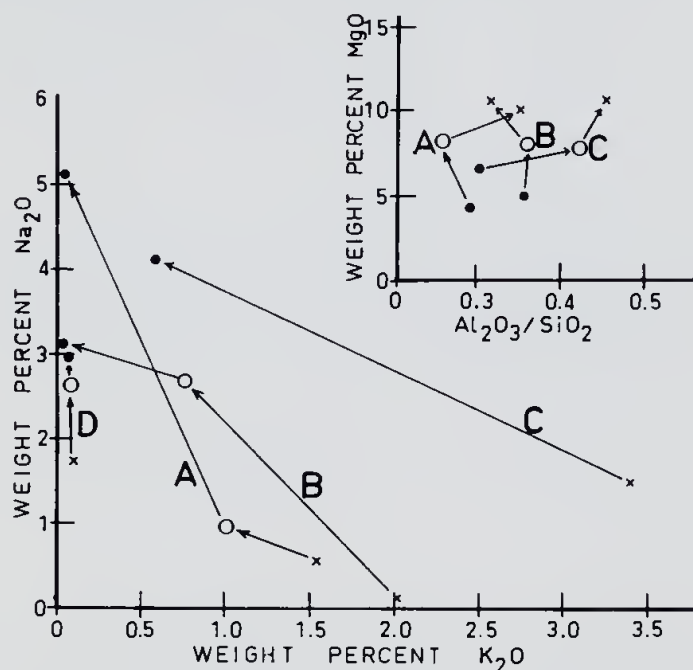


Figure 2.—Major oxide variations in spilitic pillow, Mt. Hunt. A = spilitic pillow, Mt. Hunt, B and C = spilitic pillows from the Franciscan Formation of California (Bailey *et al.* 1964), D = tholeiitic pillow, Norseman, W.A. (Hallberg, 1970). Solid circles indicate pillow cores, open circles pillow margins and x's pillow matrices.

## Discussion

Archaean spilites have been reported from Sweden and India (Valance, 1960) and from South America (Williams *et al.*, 1967). Although Archaean "greenstones" from Western Australia have been collectively referred to as spilites (Prider, 1948, 1961), this usage follows the assumption that all metamorphosed Archaean pillowed basalts are spilites, a supposition which is certainly not true for examples from Western Australia (Hallberg, 1970). The Mt. Hunt pillows may represent an isolated case of spilite development; a regional investigation of Archaean volcanic belts has disclosed no similar occurrence (Hallberg, 1970).

Spilitic magmas, autometasomatism, reaction with sea water and post-consolidation alteration have been proposed as mechanisms for producing spilites (Vallance, 1960). Some indication of the nature of the magma from which the spilites at Mt. Hunt were derived is given by their high concentration of Cr, Ni and Mg. It is unlikely that Cr and Ni could have been added to the pillows by any of the mechanisms mentioned; it can therefore be concluded that these values reflect the composition of the melt from which the pillows formed. The Cr and Ni values for the spilitic pillows are identical to those in the associated high-Mg basalts (Table 1). It is therefore postulated that the pillows were

formed from a high-Mg basalt magma and that spilitization occurred during or after pillow formation. The association of high-Mg basalts, layered sills, intrusive ultramafics and pelitic sediments is believed to represent a sequence of oceanic crustal material (Hallberg and Williams, unpublished data). That spilites can develop in such an environment is attested to by their presence in some Alpine sequences (Vallance, 1960). Perhaps the most important, and yet unanswered, question is why similar spilitic rocks have not developed in other volcanic belts in the Eastern Goldfields region deposited in similar environments.

#### Acknowledgements

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## 2.—*Erythrobatrachus noonkanbahensis*, a Trematosaurid species from the Blina Shale

by John W. Cosgriff \* and Neil K. Garbutt †

Manuscript received 27 July, 1971; accepted 19 October, 1971

### Abstract

*Erythrobatrachus noonkanbahensis*, a new temnospondyl of the family Trematosauridae, is based on three skull fragments collected at a locality in the Lower Triassic Blina Shale of the Fitzroy Trough in Western Australia. A partial restoration of the skull accomplished from these fragments indicates that the taxon belongs to the group of trematosaurids characterized by elongate, narrow skulls that includes *Aphaneramma*, *Gonioglyptus*, *Stochiosaurus* and *Wantzosaurus*. Although it is clearly and equally distinct from all of these the general relationship suggests an early Scythian age for the new form. This age is consonant with the basal Scythian stratigraphic position of the Blina Shale vertebrate fauna established by a variety of fossil evidence.

### Introduction

The three skull fragments that comprise the hypodigm of *Erythrobatrachus noonkanbahensis* are all extremely weathered, broken and incomplete. They were collected from the surface of the fossil locality, U.C.M.P. V6044 on Noonkanbah Station in the West Kimberley District (Cosgriff, 1969, fig. 1). The holotype, W.A.M. no. 62.1.46, and one topotype, W.A.M. no. 62.1.50, were found about 100 yards apart in July, 1960, by a joint field party of Western Australian Museum and the University of California, Berkeley. The second topotype, W.A.M. 71.6.22 was found by the senior author in July, 1965, during a field trip of the Department of Zoology and Comparative Physiology, Monash University, near the spot where W.A.M. no. 62.1.50 had been found five years before. W.A.M. nos. 62.1.46 and 71.6.22 are internal matrix casts from which most of the surface bone has been eroded. They retain, however, such features as traces of the sutures separating bones and casts of openings and foramina that project in relief from the core surfaces. W.A.M. no. 62.1.44 (fig. 1) is from the central region of a skull and includes partial casts of both orbits. W.A.M. no. 71.6.22 (fig. 2) is from the right posterolateral corner of a skull considerably smaller than that of the holotype. The other specimen, W.A.M. no. 62.1.50 (fig. 3) is an external impression from the palatal surface of the snout region of an individual somewhat smaller than that represented by the holotype. The impression, retained on a piece of shale matrix, shows two pairs of parallel tooth rows and a few sutures.

Although the three specimens derive from different portions of skulls not comparable in size and were found widely separated from each other there is little doubt that they are homotaxial. All are from elongate, narrow skulls. Such features as orbits, internal nares and interpterygoid vacuities closely match in general outline and relative size when compensation is made among them for overall size. In following passages each of the specimens is described separately, following which the restoration of the skull is discussed and compared with skulls of other trematosaurids.

This report is the fourth in a series appearing in this journal dealing with the vertebrate fauna of the Lower Triassic Blina Shale. The first report (McKenzie, 1961) provides a detailed description of the lithology of the unit at the vertebrate localities, a map of certain localities and an analysis of the depositional environment. The second (Cosgriff, 1965) is a consideration of the rhytidosteid temnospondyl, *Deltasaurus kimberleyensis* and the third (Cosgriff, 1969) a consideration of the brachyopid temnospondyl, *Blinasaurus henwoodi*. All three contain information on the geographic and stratigraphic positions of all of the vertebrate localities, on the total fauna and flora of the unit and on the history of collecting at the localities. In addition, the second report considers the nature of preservation of the vertebrate faunas recovered from Upper Permian and Lower Triassic units found in other parts of the world. For more detail on the general geology and stratigraphy of the unit the reader is referred to Guppy *et al.* (1958), McWhae *et al.* (1958), and Veevers and Welles (1961).

This report concludes studies on the Temnospondyli of the Blina Shale fauna. Remaining undescribed vertebrate material in the W.A.M. and U.C.M.P. collections consists mainly of scanty, incomplete and poorly preserved fish remains but also includes some large chunks of bone, perhaps from an ichthyosaur, and some enigmatic bony plates whose allocation, even to class, is uncertain. Among the fish material are tooth plates of *Ceratodus*, skull parts of *Saurichthys* and a coelacanthid and a trunk impression of an actinopterygian. Some discrepancy will be noted between these statements and the faunal listings provided by the author in the two previous accounts. The 1965 paper (p. 89) notes the presence of "... trematosaurids which are perhaps congeneric with *Aphaneramma* and *Tertrema* of the Posidonomya Beds," and the

\* Department of Biology, Wayne State University, Detroit, Michigan.

† University College of the West Indies, Kingston, Jamaica.

1969 paper (p. 65) mentions "... a capitosaurid, two trematosaurids." The "*Terrema*" of the 1965 report is actually W.A.M. no. 62.1.44 now described as the holotype of *Erythrobatrachus noonkanbahensis*, and the "*Aphaneramma*" is W.A.M. no. 62.1.50, one of the topotypes of this species. The two trematosaurids mentioned in the 1969 paper are also these two specimens. The comparisons of the two with W.A.M. no. 71.6.22, found later, establishes the homotaxy of all three and, together, they seem sufficient to form the basis for the new genus and species. The capitosaurid noted in 1969 is a lower jaw which, on further analysis, seems to be referable to *Deltasaurus kimberleyensis*.

### Order Temnospondyli

This order constitutes the principal group of the Labyrinthodontia during the interval Carboniferous through Triassic and has been extensively reviewed and classified by Case (1946), Romer (1947), Säve-Söderbergh (1935) and Watson (1919). The partial classification here adopted which concerns the Trematosauroidae is an amalgamation of Romer (1947), Säve-Söderbergh (1935), Welles and Cosgriff (1965) and Cosgriff (1965). In this the suborders of the Temnospondyli are abandoned and the various superfamilies including the Trematosauroidae are placed directly under the order. Romer (1947) divided the contents of the order among four suborders, Ichthyostegalia, Rhachitomi, Trematosauria and Stereospondyli; later (1966), he modified the classification considerably, removing the Ichthyostegalia to a separate order, demoting the Trematosauria to a superfamily (Trematosauroidae) of the Stereospondyli and retaining this last with the Rhachitomi as the only two suborders of the Temnospondyli. Welles and Cosgriff (1965), following Säve-Söderbergh (1935), abandoned these last as formal groupings, noting that: "... the line of separation between the two suborders based on the nature of the vertebrae is not so clear as was once supposed. Various members of the Stereospondyli exhibit intermediate conditions between rhachitomous and stereospondylous ossification." This variation may be observed even among genera of a single superfamily as in the Capitosauroidae. Further, as both Säve-Söderbergh and Welles and Cosgriff point out, the Triassic Stereospondyli seem to be a highly polyphyletic group possessing points of origin among a number of different groups of Permian Rhachitomi.

### Superfamily Trematosauroidae

The superfamily, as here considered, parallels Romer's (1947) Suborder Trematosauria in being monotaxial, containing only the family Trematosauridae. Romer (1966), however, followed the author (1965) in part by removing the genera *Peltostega* and *Rhytidosteus* from the Trematosauroidae and placing these with *Deltasaurus* in the reconstituted family Rhytidosteidae (von Huene, 1920). The two classifications diverge at this point, though, as Romer included the Rhytidosteidae as a second family of the Trematosauroidae and Cosgriff assigned

it to a new superfamily, Rhytidosteoidea which appears to be closely allied to the Rhinesuchoidea.

**Definition.** Romer, (1947, p. 314) provided a diagnosis of the Suborder Trematosauria which may be transferred to the Trematosauroidae and also applied to the Trematosauridae as the only contained family. Much of the diagnosis is differential in type including some characters that are typical of the entire Order Temnospondyli and some that are typical of the Triassic members of the order. The definitive characters of his diagnosis that serve to distinguish the Trematosauroidae from the other superfamilies of the order include the following:

"Skull not depressed but relatively high and narrow; triangular in shape with pointed snout; frequently elongate both pre- and post-orbitally."

"Body of the parasphenoid developed as a broad and elongate plate extending backward below occipital region; fused basal articulation exhibits long suture between parasphenoid and pterygoid."

"Exoccipital-ptyergoid contact present but not visible ventrally."

The diagnosis of the family provided by Säve-Söderbergh (1935, p. 87) concurs with that of Romer in most respects although it expresses the above characteristics in different terms. One character listed in this that should be added to the above is:

"Processus cultriformis of the parasphenoid very high and narrow."

All of these characters could probably be validated through quantitative comparisons among the superfamilies of the Temnospondyli. This, however, would be beyond the scope of the present paper and they are accepted for the present purpose of determining the taxonomic position of the new form from the Blina Shale.

### Family Trematosauridae

The Trematosauridae, confined to the Lower Triassic (and perhaps, the uppermost Permian), occur in continental deposits of Arizona, Germany, Russia and South Africa and in marine or marginal deposits of Australia, Greenland, India, Madagascar and Spitzbergen. The family seemingly experienced a considerable evolutionary radiation just before and during its short range in the stratigraphic record. In number of genera it is the largest of the Temnospondyl families of the Triassic. These genera although showing great diversity in skull shape and proportions obviously constitute a natural and well-defined group through the distinctive features set forth in diagnoses of Romer and Säve-Söderbergh.

The osteology of the skull and the lower jaw of several of the better-known species has been thoroughly studied and well-documented by a number of investigators. A review of this work together with excellent summaries of the morphology of the species has been provided by Romer (1947).



*Contents of the family.* The species reviewed by Romer (1947) and considered by him to be valid taxa of the Trematosauridae include: *Trematosaurus brauni* (Burmeister, 1849) from the middle Buntsandstein of Western Germany; *Trematosaurus* sp. (Sushkin, 1927) from Zone VI of the Cis-Uralian region of the U.S.S.R.; "*Trematosaurus*" *kannemeyeri* (Broom, 1909), *Trematosuchus sobeyi* (Haughton, 1915), *Microsaurus casei* (Haughton, 1925) and *Rhytidosteus capensis* (Owen, 1884), all from the Cynognathus Zone of South Africa; *Aphaneramma rostratum* (Woodward, 1904), *Peltostega erici* (Wiman, 1916), *Peltostega wimani* (Nilsson, 1946), *Platystega depressa* (Wiman, 1915), *Lyrocephalus euri* (Wiman, 1914) and *Tertrema acuta* (Wiman, 1915), all from the Sticky Keep Formation of Spitzbergen; *Lyrocephalus kochi* (Säve-Söderbergh, 1935) and *Stochiosaurus nielsenii* (Säve-Söderbergh, 1935), both from the Woody Creek Formation of Greenland; *Gonioglyptus longirostris* (Huxley, 1965) from the Panchet beds of Bengal, India; and *Gonioglyptus kokeni* (Huene, 1920) from the Prionolobus beds of the Salt Range of India. Most of these species are based on adequate cranial material but "*Trematosaurus*" *kannemeyeri* and *Gonioglyptus longirostris* are, as Romer notes, dubious taxa founded on very fragmentary specimens. The species of *Peltostega* and *Rhytidosteus* as noted in a previous section, have been removed from the family.

Species that have been described since 1947 and that are added to the family in Romer's (1966) text include: *Inflectosaurus amplius* (Shishkin, 1960) from Zone V of the Cis-Uralian region of the U.S.S.R. and *Wantzosaurus elongatus* (Lehman, 1961) from the Middle Sakmena beds of Madagascar. This listing also includes with question *Laidleria gracilis* (Kitching, 1957) from the Cynognathus Zone of South Africa. Kitching placed this form in its own family under the Stereospondyli and the senior author (1965) suggested that this family, Laidleriidae, could be included provisionally in the Rhytidosteidae.

Lehman (1966) added the following species from the Middle Sakmena beds to the family: *Trematosaurus madagascariensis*; *Aphaneramma* sp.; *Ifasaurus elongatus*; and *Lyrosaurus australis*. Of these, only the first appears to be a valid taxon founded on adequate material. *Ifasaurus elongatus* and *Aphaneramma* sp., although trematosaurids without doubt, are based on skull fragments with a few distinctive features. *Aphaneramma* sp. resembles *Wantzosaurus elongatus*. *Lyrosaurus australis* closely resembles *Mahavisaurus dentatus*, a form described and illustrated by Lehman in this paper which, however, he placed with question in the Rhinesuchoidea.

#### **Erythrobatrachus,\* gen. nov.**

*Type species.* *Erythrobatrachus noonkanbahensis*.

*Differential diagnosis.* A long-snouted, slender-skulled trematosaurid (allied to *Aphaneramma*

*rostratum*, *Gonioglyptus kokeni*, *Stochiosaurus nielsenii* and *Wantzosaurus elongatus*) with proportionately small interpterygoid vacuities distinguishing it from all of these—length of interpterygoid vacuities as measured on midline only about three-fourths of length of posterior part of skull roof as measured on midline from level of anterior borders or orbits to posterior edge of skull roof. It is further distinguished from *A. rostratum* and *W. elongatus* through being relatively short and broad in the region of the skull roof bounded by orbits, external nares and lateral skull margins—width of skull across anterior margins of orbits between eight-tenths and nine-tenths of length as measured on midline between anterior borders of orbits and posterior borders of external nares. It resembles *A. rostratum* and *W. elongatus* but differs from *G. kokeni* and *S. nielsenii* in showing very little increase in skull width posterior to the orbits—width of skull across posterior margins of orbits about eight-tenths of greatest width of skull across posterolateral corners. Lateral margins of skull bulged outward in orbital region following curvature of orbit lateral borders as in *G. kokeni*, a feature not observed in the other three species.

#### **Erythrobatrachus noonkanbahensis, sp. nov.**

*Holotype.* W.A.M. no. 62.1.46, an internal matrix cast of the central region of a skull.

*Type locality.* U.C.M.P. locality V6044, Noonkanbah Station, West Kimberley District, Western Australia. The approximate position is shown on a map in Cosgriff (1969, Fig. 1, p. 66) and it is the same locality as the site listed by McKenzie (1961, p. 73, Table II, ninth entry) as: "Bore G, Noonkanbah Station, 124° 45' E., 18° 20' S." To reach the site drive about 15 miles south from Calwynyardah homestead on the station road leading to Noonkanbah homestead to a spot where a fence and fence road cross the station road. Turn east onto the fence road and drive about  $\frac{3}{4}$  mile. The locality, which lies about  $\frac{1}{2}$  mile north of this point, is a low rounded hill approximately 150 yards in diameter. To give another reference point, it lies about  $1\frac{1}{2}$  miles N70E from Noonkanbah Station Bore no. 20 which is on the west side of the Calwynyardah-Noonkanbah Station road. The hill is capped with a remnant of the Quaternary Warrimbah Conglomerate and its flanks are covered with a scree of pebbles of varied lithology which become smaller in size and more widely spaced toward the base of the hill. Some of the pebbles closely resemble samples of the Blina Shale from the Erskine Range; some resemble samples of the Erskine Sandstone from this area; and some have been ferruginised beyond recognition.

*Horizon.* Blina Shale, the upper portion of this unit, Otoceratan Division of the Scythian State.

*Topotypes.* W.A.M. no. 71.6.22 an internal matrix cast of the right posterolateral portion of

\*Genus name from Gr.: erythro-red, plus, batrachos-frog; it is given in reference to the iron-stain colour of the specimens.

a skull. W.A.M. no. 62.1.50, the impression of the palatal surface of the snout region of a skull, broken off across the anterior margins of the internal nares.

*Diagnosis.* As for genus.

#### Description

W.A.M. no. 62.1.46. The type specimen, primarily a matrix core, is derived from the central region of a skull. It is broken off through the centers of the orbits and immediately posterior to the external nares. The impressions of dermal bones are retained on the dorsal and palatal surfaces. Internal sutures are marked by serrate ridges in low relief. The matrix casts of the anterior portions of the orbits and interpterygoid vacuities and the cylindrical infillings of various small foramina project from the core surface.

A fragment of dermal bone remains on each side of the core of the rostrum. The fragment on the left side is the more extensive and includes parts of the maxillary and palatine bones. The palatal surfaces of these bones about the edges of the core and enclose the entire left choana.

A patch of eroded bone covered a small area of the dorsal surface anterior to the left orbit. This was removed in order to locate the internal sutures on this part of the core.

The internal core rapidly narrows from the centers of the orbits to a constriction midway between the orbits and external nares. The specimen widens abruptly anterior to this constriction but much of this width is contributed by the fragments of dermal bone on the sides of the rostral core. The rostral core, itself, gradually decreases in width anterior to the constriction. The constriction of the snout was probably reflected in a more moderate fashion, on the external surface of the original skull.

*Dorsal surface* (fig 1a). The orbital casts have oval anterior borders. They lie close to the lateral edges of the core. The cast of the left orbit is more complete and has an everted rim. The dermal bone surrounding the left orbit was 5-6 mm. thick.

The frontal impressions are of nearly even width from front to back and are excluded from the medial margins of the orbits by the postfrontal and prefrontal impressions. The frontal-nasal sutures are quite jagged.

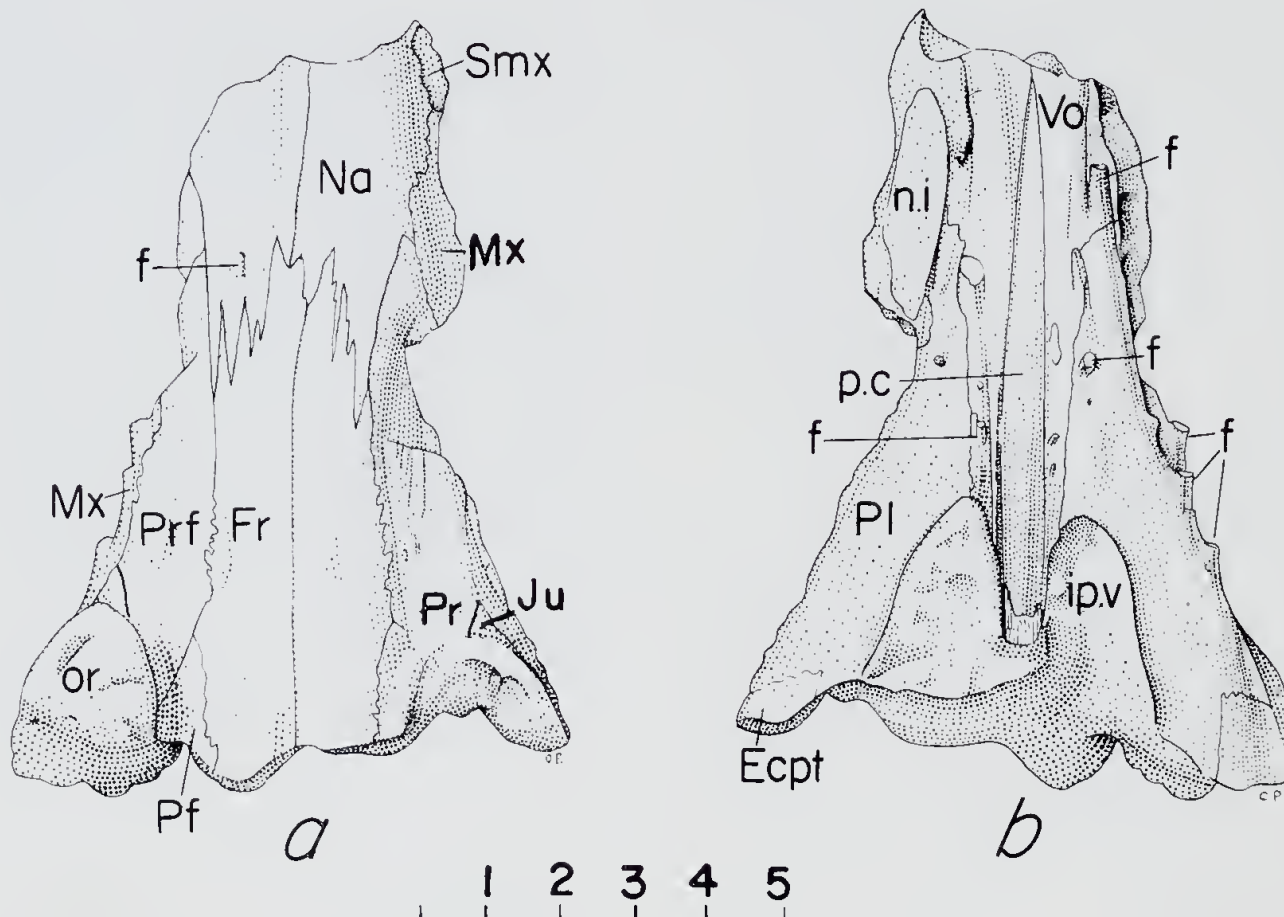


Figure 1.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov., holotype, W.A.M. no. 62.1.46; a. dorsal view; b. ventral view.

Abbreviations for Figure 1 and following Figures: Ec, Ecpt, ectopterygoid; Eo, exoccipital; f, foramen; f.p, parietal foramen; fl, descending flange of postfrontal; fo, st, subtemporal fossa; Fr, frontal; ip. v, interpterygoid vacuity; Ju, jugal; Mx, maxillary; max. t, maxillary teeth; n.e, external naris; n.i, internal naris; Na, nasal; or, orbit; P, parietal; p.c, cultriform process of parasphenoid; pal. t, palatine tusk; Pf, post-frontal; Pl, palatine; Pm, pre-maxillary; Po, postorbital; Pp, postparietal; Pr, Prf, prefrontal; Ps, parasphenoid; Pt, pterygoid; Qu, quadrate; Quj, quadratojugal; Smx, septomaxillary; Sq, squamosal; St, supratemporal; Tab, tabular; Vo, vomer.



The nasal impressions are broader than the frontal impressions. The internasal suture is off-set to the left of the interfrontal suture. The right nasal impression is laterally bordered by the impressions of the prefrontal, maxillary and septomaxillary bones. The left nasal has the cylindrical infillings of two small foramina projecting from its surface.

The prefrontal impressions form the antero-medial borders of the orbits. They have medial sutures with the postfrontal and frontal impressions and lateral sutures with the jugal and maxillary impressions. They have pointed anterior borders which are level with the anterior terminations of the frontal impressions.

Only the anterior corners of the postfrontal and jugal impressions are present on the dorsal surface. They are laterally bordered by the maxillary impressions. The postfrontal impressions form the medial margins of the orbits. The jugal impressions form the lateral and anterolateral borders of the orbits.

Narrow strips of maxillary impression lie along the lateral edges of the core. Two of these strips flank the prefrontals and jugals in the posterior portion of the specimen. A third piece of maxillary impression lies lateral to the right nasal impression. The maxillary impression of the left side has three large infillings projecting forward along its lateral edge; these perhaps represent foramina for branches of nerve V2.

The posterior apex of the right septomaxillary rests on the maxillary fragment and is medially bordered by the nasal impression. The septomaxillary is never an extensive bone and the external nares must have lain close to the broken anterior margin of the core.

*Palatal surface* (fig. 1b). Only the anterior portions of the interpterygoid vacuity cores are preserved. They are narrow with rounded anterior borders. The dermal bone at the anterior border of the right vacuity was 1-2 mm. thick.

The right choana is a symmetrical opening, 2.6 cm. long and 0.6 cm. wide across its center. It is enclosed within the fragments of the maxillary and palatine bones and lies close to the lateral edge of the internal core.

The impression of the cultriform process of the parasphenoid runs up the center of the palatal surface. The termination is level with the anterior edge of the choana. The anterior portion of the cultriform process had a flat upper surface. Posterior to the region of the choana the upper surface becomes progressively more concave. Most of the left parasphenoid-vomer suture is clearly marked.

Each vomer-palatine suture follows an irregular course from the medial edge of the choana back to the antero-medial border of the interpterygoid vacuity. The impressions of the vomer and palatine bones are rippled and striated, reflecting the texture of the upper surfaces of the bones.

The impression of the left vomer extends down the length of the fragment lateral to the

parasphenoid impression. The anterior and posterior edges of the impression are missing. It is flat-lying in the region medial to the choana. Posteriorly, the vomer impression narrows and becomes vertical on the medial border of the interpterygoid vacuity. The position of this portion of the vomer impression between parasphenoid impression and interpterygoid vacuity shows that the cultriform process of the parasphenoid was flanked by processes of the vomer bones.

Two forwardly-directed cylinders of which the anterior is the largest protrude from the surface of the vomer impression just within the left vomer-palatine suture. One or both of these may correspond with the foramen of *Lyrocephalus euri* which Säve-Söderbergh (1936, figs. 4 & 5) labelled "the posterior opening in the vomer for the palatine nerve".

The anterior terminations of the palatine impression lie on the medial sides of the choanae. Posteriorly, the impressions are limited by the broken edges of the core and by the anterior corners of the ectopterygoid impressions. The lateral edges of the palatine impressions could not be located and the relationships with the maxillary impressions and the impressions of other bones of the skull roof are unknown.

Each palatine impression has a small round protuberance posterior to the choana. These are infillings of foramina which may correspond to the *foramina recti palatonasalis* of *Lyrocephalus euri* and *Aphaneramma rostratum*, so designated by Säve-Söderbergh (1936, figs. 4, 5 and 34).

A small portion of ectopterygoid impression remains on each posterolateral corner of the palate surface. The left impression is the largest. It has a rounded anterior border with a tightly serrate suture on the palatine impression.

W.A.M. no. 71.6.22. This specimen, a second matrix core, is derived from the right posterolateral region of a skull. The individual represented by this fragment was considerably smaller than the individual represented by the holotype, probably less than half its size. The fragment ends anteriorly at an irregular break that crosses the dorsal surface just anterior to the posterior margin of the right orbit and that crosses the palatal surface through the approximate centre of the right interpterygoid vacuity. The broken medial surface is also quite irregular but, in general, slopes dorsolaterally so that the preserved portion of the palatal surface is more extensive than the preserved portion of the dorsal surface. The lateral and posterior edges are, for the most part, the complete, natural edges of the matrix core although the posterior portion of the lateral edge, the part bordering the subtemporal fossa, is chipped in a few places.

The dorsal surface is entirely internal cast portraying the nearly smooth inner surface of the skull roof with sutures marked as a slightly raised ridges. The occipital surface contains only the right posterior cheek wall, largely composed of internal cast surface but retaining a part of the quadrate bone ventrally. The



palatal surface was originally covered by hematite-rich matrix. This was prepared off, revealing the nearly complete subtemporal fossa, the posterior half of the interpterygoid vacuity and large parts of the parasphenoid, pterygoid and quadrate bones. The latter are poorly preserved and splintery. The medial surface is a break crossing the right lateral area of the braincase.

**Dorsal surface** (fig. 2A). The smooth internal cast surface curves sharply down from the broken medial edge to the lateral margins. The posterior margin, formed completely by the edges of the quadratojugal and squamosal bones, is slightly convex posteriorly. From this point, the dorsal surface narrows gradually forward to the posterior margin of the orbit.

Only one complete and four partial impressions occupy the dorsal surface. The postorbital impression is of nearly even width from its smoothly curved border on the right orbit to its posterior termination. It ends at the medial break surface, probably just lateral to its original sutural border on the postfrontal and supratemporal impressions. Laterally it ends with sutural traces separating it from the jugal and quadratojugal impressions.

The squamosal is the largest impression, making up nearly a third of the dorsal surface of the specimen. It has extensive sutural contact with the quadratojugal, jugal and postorbital as shown in the illustration. As with

the postorbital it has a jagged medial edge, being broken off just lateral to its sutural union with the supratemporal and tabular elements.

Only the posterior part of the jugal impression is retained. It forms the lateral and part of the posterior margins of the orbit and, from these, extends back to a sutural trace separating it from the quadratojugal. Its medial edge on the subtemporal fossa is somewhat chipped.

The surface of the quadratojugal, the only complete impression on the dorsal surface, extends from the jugal sutural trace to the posterior edge and from the margin of the subtemporal fossa to the squamosal sutural trace.

A small corner of the postfrontal impression is probably present posterior to the orbit margin and anterolateral to the postorbital as this is part of the area of the skull normally occupied by the postfrontal in temnospondyls. However, a sutural trace dividing it from the postorbital is not retained.

**Palatal surface** (fig. 2B). This surface, in a fair state of preservation, is broken off laterally just to the left side on the cultriform process and, anteriorly, through the centre of the interpterygoid vacuity.

The two most prominent features of the palatal surface are the interpterygoid vacuity and the subtemporal fossa. The preserved part of the interpterygoid vacuity is long and narrow. It has a straight medial margin throughout and the lateral margin is very slightly convex in its anterior part. The posterior part of the lateral margin is slightly indented by the convex edge of the palatal ramus of the pterygoid bone. The width of the vacuity is 17 mm. at its broken anterior edge and only 7 mm. in the area where it is indented by the pterygoid.

The subtemporal fossa appears as an elevated matrix platform due to the loss of most of the surrounding bone. It is long and narrow as is usual for the trematosaurids, measuring 39 mm. in maximum length and 13 mm. in maximum width. The lateral border, formed by the quadratojugal and jugal, is nearly straight and the medial border, formed by the pterygoid, is slightly concave on its anterior half and straight on its posterior half. The anterior margin which lies about 10 mm. anterior to the posterior margin of the interpterygoid vacuity is evenly rounded. The posterior border is formed by a poorly preserved portion of the quadrate condyle and is inclined diagonally in a posterolateral direction.

Besides the quadrate the only bone preserved on the palatal consists of portion of the parasphenoid and the right pterygoid. The parasphenoid portions include the right lateral part of the basal plate and the posterior part of the cultriform process. The approximate position of the parasphenoid-ptyerygoid suture is indicated by a change in direction of bone grain and runs posterolaterally from the posterior margin of the interpterygoid vacuity to the broken posterior edge of the specimen. The cultriform process, a very narrow structure as in all trematosaurids, is poorly preserved with edges that are discontinuous and indistinct in places.

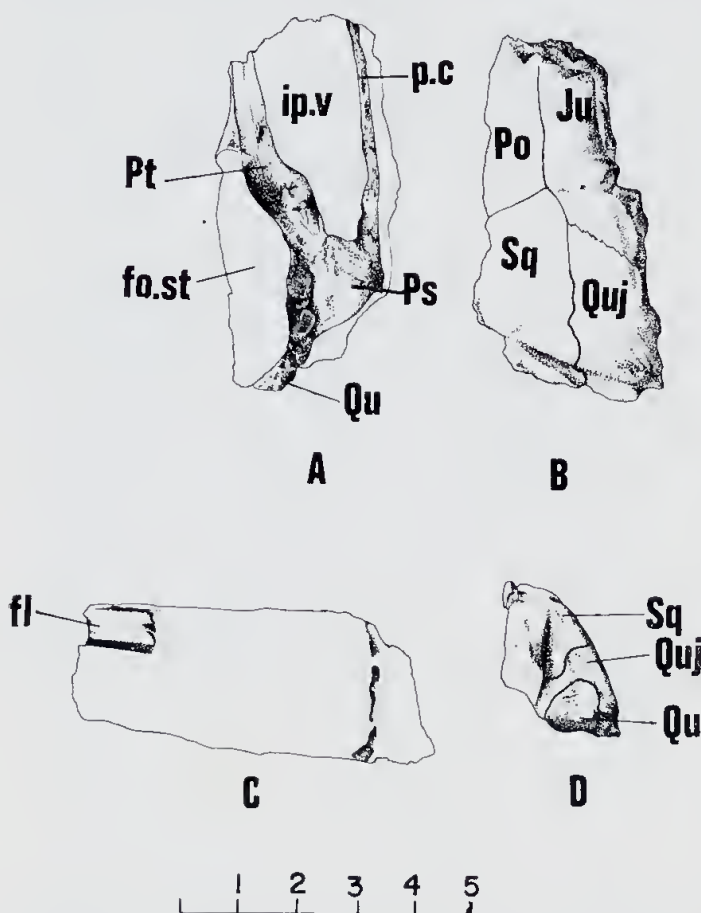


Figure 2.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov., topotype, W.A.M. no. 71.6.22. A. ventral view; B. dorsal view; C. medial view; D. occipital view.

**Occipital surface** (fig. 2C). The internal impression of the posterior cheek wall retaining a weathered remnant of the quadrate bone is the only portion of this surface retained on the specimen. In rear view this impression is triangular in outline with an apex at the locus of the missing otic notch and slightly concave in shape. It lies in a plane nearly normal to the dorsal surface of the specimen and slopes posteriorly, ventrally and laterally to the region of the articular surface of the quadrate bone. The lateral edge meets the dorsal surface impression at nearly a right angle and the medial edge is free, forming the lateral margin of the pteroccipital fenestra. The clearly marked trace of the squamosal-quadratojugal suture runs transversely across the middle of the impression surface. The remnant of quadrate bone is missing all of its surface and is nothing more than an irregular lump of ferruginized material occupying the ventral part of the concavity of the cast surface.

**Medial surface** (fig. 2D). The only feature identified with certainty on this surface is the impression of the descending flange of the right postfrontal bone. (See S  ve-S  derbergh, 1936, fig. 10 for a portrayal of this structure in *Lyrocephalus euri*.) It is a cylindrical, medially convex structure, 14 mm. in length and 8 mm. in depth. It slopes ventromedially from the edge of dorsal surface and ends in a straight free margin that lies 7 mm. directly above the dorsal surface of the cultriform process of the parasphenoid bone. The space between the postfrontal flange and the cultriform process was occupied by an entirely cartilaginous sphenethmoid bone as no trace of ossification is retained in the area.

Posterior to the postfrontal flange the medial surface of the specimen is badly eroded, containing a number of deep irregular pits (not shown in the figure). Some of these may be, in part, impressions of the outer surfaces of such internal structures as the basisphenoid, epipterygoid, prootic, opisthotic and exoccipital bones. They are, however, so weathered and incomplete that attempts at identification and reconstruction would be speculative at best.

W.A.M. no. 62.1.50 (fig. 3). The impression is from an 8 cm. length of a very slender rostrum anterior to the choanae; an unknown amount of the tip is lacking. It is 3 cm. broad at the posterior end and 1.4 cm. broad at the anterior end. The dentition and other features are hard to trace on the impression but stand out in clear relief on a latex peel.

The anterior borders of the left choana indicates that this opening was oval in shape and slightly broader than the choana of W.A.M. no. 62.1.46. The edge of the right choana is compressed and pushed forward from its original position.

Four rows of small, closely spaced teeth extend forward from the choana to the anterior break on the edge of the fragment. The medial rows are on the vomer bones and border each other on the midline. The lateral rows are on the maxillaries (and, perhaps, in part, on the

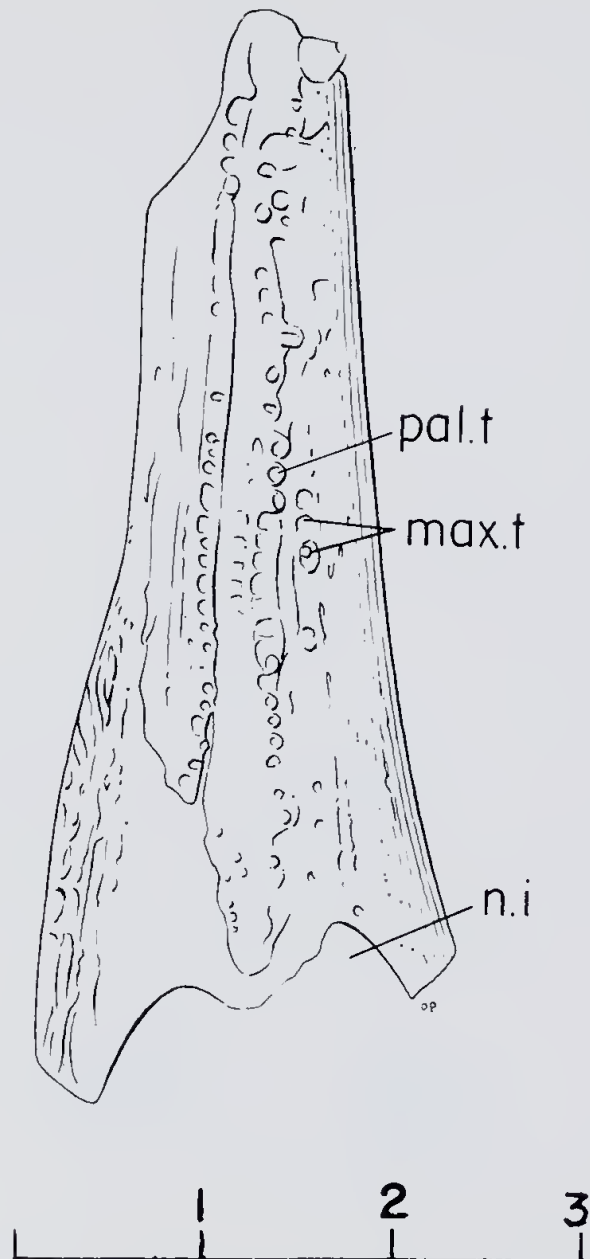


Figure 3.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov., topotype W.A.M. no. 62.1.50, palatal view of latex peel.

premaxillaries as well), and are separated from the medial rows by narrow fissures. These fissures probably represent the maxillary vomer sutures.

The right posterior part of the maxillary retains an impression of the surface sculpture, a pattern of small, irregular pits.

#### Restorations of the skull

Comparisons among the three skull specimens indicate that they are homotaxial although the two topotypes were clearly derived from individuals considerably smaller than the animal represented by the holotype. Although each specimen comes from a different area of the skull the two topotypes each possess certain features that compliment or coincide with

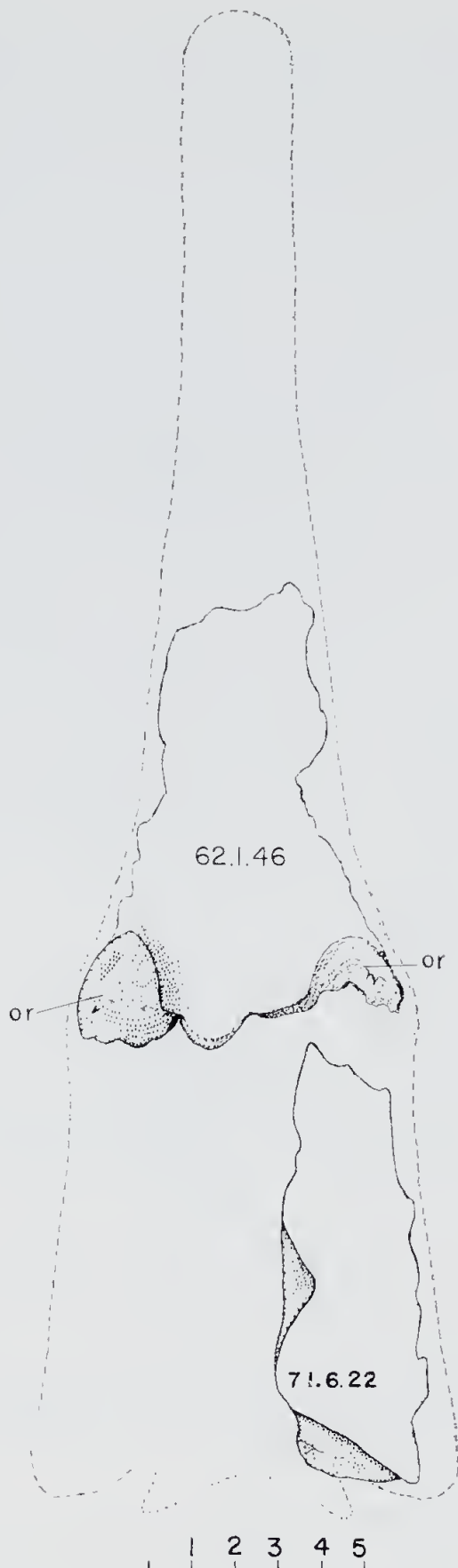


Figure 4.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the dorsal surface of the skull, showing the topographical relationships of the two specimens, W.A.M. nos. 62.1.46 and 71.6.22, to each other.

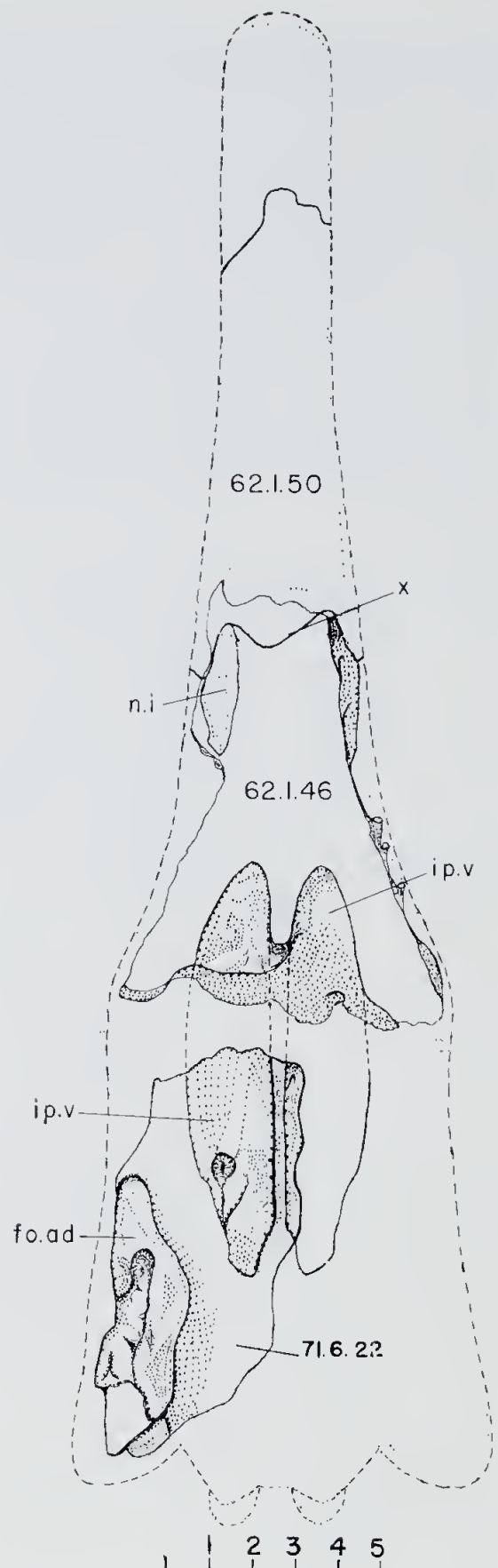


Figure 5.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the palatal surface of the skull showing the topographical relationships of the three specimens, W.A.M. nos. 62.1.46, 62.1.50 and 71.6.22, to each other.



features retained by the holotype. Partial restoration of the skull of *Erythrobatrachus noonkanbahensis* are attempted (figs. 4-7) and the results show a long, narrow trematosaurid skull of the *Aphaneramma* type (Säve-Söderbergh, 1936, figs. 31-33).

The basic restorations (figs. 4 and 5) show the topographical relationships of the three specimens to each other in dorsal and palatal view and also the outlines of the original skull as extrapolated from this arrangement of the specimens. In devising these restorations W.A.M. 62.1.46 and W.A.M. 71.6.22 were enlarged X2 to make them comparable in size to the holotype. As shown in the figures there is a slight overlap of portions preserved on W.A.M. 62.1.50 with portions preserved on the holotype but no overlap in preserved portions between the latter and W.A.M. 71.6.22.

The more complete restorations (figs. 6 and 7) are attempts to portray most of the internal cast surface of an individual comparable in size to that represented by the holotype. These show such features as the restored shapes of the orbits, external nares, and also the traces of the sutures of the internal cast surfaces. The restoration of the palate also includes those portions of the maxillary and vomerine tooth rows retained as impressions on W.A.M. 62.1.50.

The features of W.A.M. 62.1.50 that indicate that it is homotaxial with the holotype and that it should be positioned as shown in fig. 5 concern the trends of its lateral margins and the position of its internal nares. As observed on the holotype the rapid convergence of the margins of the cast surface in the region of the internal nares, matched by the angle at which the right internal naris converges on the skull midline, definitely shows that the original complete skull terminated anteriorly in a very long, slender, prenasal rostrum. This anticipated shape for the rostrum is realized closely by the impression surface of W.A.M. 62.1.50. With X2 enlargement of this specimen a nearly exact fit is achieved with the broken anterior edge of the holotype. This fit is further confirmed by the matching of the borders of the internal nares of the two specimens. As noted in the description the anterior margins of both internal nares are present on the W.A.M. 62.1.50 impression. They have been somewhat deflected to the left through postmortem distortion of the specimen but, when restored to their natural positions, the right margin coincides with the anterior margin of the right internal naris of the holotype and the left margin falls near the position the anterior margin of the missing left internal naris of the holotype would have occupied.

The features of W.A.M. 71.6.22 that indicate it is homotaxial with the holotype and that it should be positioned as shown in figs. 5 and 6 concern the relative sizes, positions and shapes of the orbits, interpterygoid vacuities and cultriform processes of the parasphenoid bones. In this topotype a portion of the posterior margin of the right orbit is retained on its anterior break surface. With X2 enlargement it can be

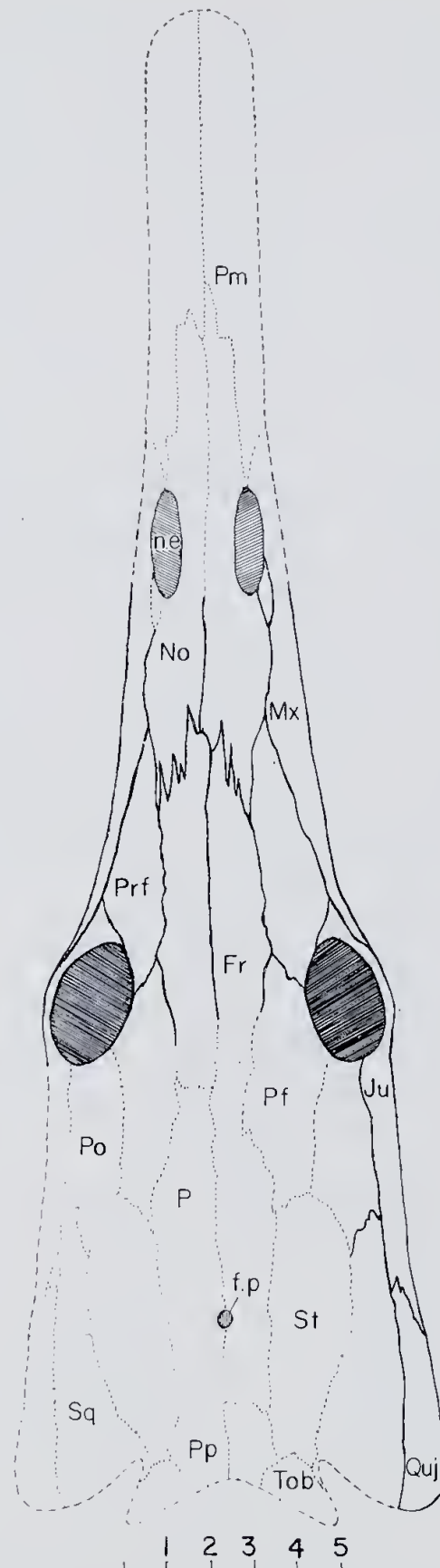


Figure 6.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the dorsal surface of the skull, based on the two specimens, W.A.M. nos. 62.1.46 and 71.6.22, and showing the restored outlines of the skull, restored shapes of the orbits and external nares and the traces of sutures on the internal cast surfaces.

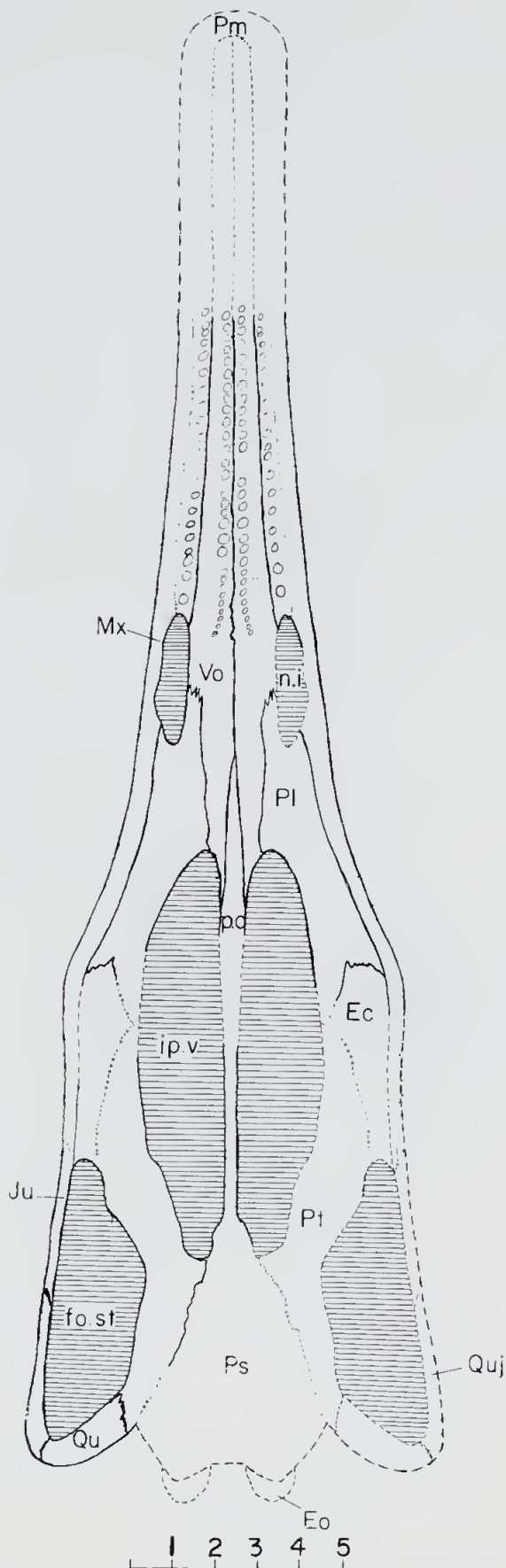


Figure 7.—*Erythrobatrachus noonkanbahensis*, gen. et sp. nov. Restoration of the palatal surface of the skull, based on the three specimens, W.A.M. nos. 62.1.46, 62.1.50 and 71.6.22, and showing the restored outlines of the skull, restored shapes of the subtemporal fossae, interpterygoid vacuities and internal nares. The sutures indicated on the postnasal region are from the internal cast surfaces but the sutures on the prenasal region are the actual external expressions.

seen that this margin represents an orbit comparable in relative size to the orbits represented by their anterior margins on the holotype. The orbits of the two specimens further correspond in that they occupy very lateral positions on the skulls, just internal to the margins of the core surfaces. In similar fashion the posterior part of the right interpterygoid vacuity preserved on the holotype closely resembles the anterior part of the right interpterygoid vacuity preserved on the holotype. As seen in fig. 5 the interpterygoid vacuity portions of the two specimens possess very similar shapes, the one forming a nearly exact mirror image of the other. The medial margins of both are nearly straight and the lateral margins possess the same degree of convexity. Also, the width of this vacuity relative to overall skull width in the orbital region is nearly identical in the two specimens,

W.A.M. 71.6.22 was positioned as shown in figs. 5 and 6 by aligning its cultriform process (which lies in the sagittal axis of the skull) with the cultriform process of the holotype and by placing its posterior orbit margin in such a position as to complete the oval shape of the orbit indicated by the anterior, medial and lateral margins of this opening on the holotype. The lateral margins of the composite restorations of the skull are shown in dashed line. These are drawn to follow the edges of the internal cast pieces with a small amount of extra width added to compensate for missing layers of dermal bone.

The final restoration (figs. 6 and 7) are attempts to summarize all that can be determined of the skeletal anatomy of the skull. They actually represent composite portrayals of the inner and outer surfaces of the dermal bone layer of the skull. Some features such as the outer edges, the margins of the various vacuities and openings and a section of dentition on the palatal surface portray the outer surface of the dermal bone layer. Most of the sutures, on the other hand, are placed according to the trace of their inner surfaces on the core specimens, W.A.M. 62.1.46 and 71.6.22. Regarding some of the more notable features of the skull, their shapes and positions are based on the specimens as follows: orbits, interpterygoid vacuities and cultriform processes on W.A.M. 62.1.46 and 71.6.22; internal nares on W.A.M. 62.1.46 and subtemporal fossae and quadrate regions on W.A.M. 71.6.22. The positions of the external nares are generally established by the fragment of septomaxillary bone impression retained on W.A.M. 62.1.46. They are given the long, oval shape seen in *Aphaneramma* sp. 2. (Säve-Söderbergh, 1936, p.14, fig. 1) and other trematosaurids.

The portions of the skull that are entirely hypothetical, being constructed from linear trends present on the specimens and from conditions in other trematosaurids include the snout tip, the tabular horns, the otic notches, the parietal foramen, the posteromedial portion of the palatal surface in the region of the parasphenoid corpus and the exoccipital condyles.



Almost all of the pattern of sutures shown is included only for aid in visualizing how the entire internal core surface of a skull of the species might have looked. The only sutures included which portray conditions on the outer surface of the dermal bone are the intervomerine and vomer-maxillary in the region anterior to the internal nares. These are taken from palate impression, W.A.M. 62.1.50. The dotted lines lateral to the vomer-maxillary sutures indicate the approximate boundaries between the sculptured bone of the sides of the snout from the smooth, tooth-bearing bone of the palate surface. In regard to all other sutures those that are shown in solid line are definitely established by the specimens and those that are shown in dashed line are either hypothetical or are taken as mirror-images from a definitely established suture on the opposite side of the skull. Not even the definitely established sutures are of use in taxonomic and comparative considerations as it is well known (e.g. S  ve-S  derbergh, 1936) that the internal traces of skull sutures differ considerably from their expressions on the outer surfaces of the dermal bone.

#### Comparisons with related species of the Trematosauridae

The narrowness of the skull, the attenuated rostral region and the slender cultriform process of the parasphenoid limit comparisons of the restorations of *Erythrobatrachus noonkanbahensis* (figs. 6 and 7) to two temnospondyl families, the Archegosauridae of the early Permian and the Trematosauridae of the early Triassic. The referral of the new species to the latter family is assured, however, by the construction of the basal region of the palate surface, preserved on W.A.M. no. 71.6.22. In this specimen, as in all trematosaurids and, indeed, all Triassic temnospondyls, the pterygoid bones are solidly fused to the corpus of the parasphenoid through extensive sutural unions. In the archegosaurids, as in many other groups of Permian Temnospondyli, moveable joints are found in this region between the pterygoids and the basisphenoid and the former bones lack sutural union with the parasphenoid.

An additional resemblance to other trematosaurids and contrast of archegosaurids, possessed by *E. noonkanbahensis* concerns the positions of the orbits relative to the interpterygoid vacuities. In W.A.M. no. 62.1.46, as in other trematosaurids, the orbits lie close to the anterior margins of the interpterygoid vacuities. In archegosaurids, however, the orbits overlies the posterior portions of the interpterygoid vacuities.

Possibilities for comparisons of *E. noonkanbahensis* with other trematosaurid species are restricted by the incompleteness and poor preservation of the three specimens comprising its hypodigm. Only a few general characteristics established by the restorations of the skull (figs. 6 and 7) can be utilized in attempting to establish the taxonomic position of the new form. These include, principally, the general shape and proportions of the skull and the relative

sizes, shapes and positions of its larger openings—orbis, external and internal nares, interpterygoid vacuities and subtemporal fossae. Superficial features such as development and topography of the lateral line grooves, texture of sculpture on the skull roof bones and shape, spacing and arrangement of the tooth rows, features often of taxonomic value within temnospondyl families, are either entirely lacking or are too limited in extent of preservation on the three specimens to be of use in determining relationships. The pattern of sutures dividing the dermal bones of the skull are also useless in this endeavor as it is preserved only as internal traces on W.A.M. 62.1.46 and 71.6.22 and is very restricted in extent on W.A.M. no. 62.1.50.

The trematosaurid genera divide roughly into three groups according to general skull shape: 1) those with extremely narrow, elongate skulls and a rostrum that is very extensive in the prenasal region, i.e. *Aphaneramma*, *Gonioglyptus*, *Stochiosaurus* and *Wantzosaurus*; 2) those with moderately elongate skulls and a rostrum that is not extensive in the prenasal region, i.e. *Inflectosaurus*, *Platystega*, *Microposaurus*, *Trematosaurus*, *Trematosuchus* and *Tertrema*; and 3) an isolated genus, *Lyrocephalus*, with a short, nearly triangular skull. A thorough review of the family, beyond the scope of this paper, might conclude by establishing subfamily rank for each of these three groups. Subfamilies corresponding to these groups for the most part were provisionally proposed by S  ve-S  derbergh (1935, pp. 85-87 and 200).

It is obvious, without further elaboration, that *E. noonkanbahensis* clearly belongs to the first of the groups. The morphologic evidence available, however, is insufficient for determining its exact phylogenetic position within the group. The few available characters that seem to have taxonomic significance do not conclusively show a closer relationship to any one of the genera *Aphaneramma*, *Gonioglyptus*, *Stochiosaurus* and *Wantzosaurus* than to the others. These characters, all of which are quantitative, are summarized above in the diagnosis of the genus *Erythrobatrachus* and below in Table 1.

The interpterygoid vacuities of *E. noonkanbahensis* are comparatively small relative to the length of the posterior portion of the skull roof. The length of the interpterygoid vacuities as measured on the midline is only about eight-tenths of the length of the skull roof as measured in the midline from the level of the anterior margins of the orbits to the posterior edge. In *Gonioglyptus kokeni* these linear measurements are approximately equal. In *Aphaneramma rostratum* the interpterygoid vacuities are about one-fifth longer than the skull roof linear measurement and in *Wantzosaurus elongatus* the interpterygoid vacuities are two-fifths longer.

The skull of *E. noonkanbahensis* is relatively shorter and broader in the region bounded by the orbits, external nares and skull lateral margins than is the case in *A. rostratum* and *W. elongatus*. In the Australian species the width across the anterior margins of the orbits is



Table 1

Measurements and Indices	<i>Erythrobatrachus noonkanbahensis</i>	<i>Aphaneramma rostratum</i> Säve-Söderbergh 1936, figs. 31	<i>Wantzosaurus elongatus</i> Lehman, 1961, plates 1b	<i>Gonioglyptus kokeni</i> Huene, 1920, figs. 6 and 7	<i>Stochiosaurus nielsenii</i> Säve-Söderbergh 1935, fig. 55
(A) Length from anterior margins of orbits to posterior edge as measured on the midline ....	124 mm.	60 mm.	69 mm.	122 mm.	....
(B) Length of Interpterygoid vacuities as measured on the midline ....	97 mm.	67 mm.	97 mm.	118 mm.	....
(C) Length from posterior borders of external nares to anterior borders of orbits as measured on midline ....	79 mm.	57 mm.	81 mm.	....	....
(D) Width across anterior margins of the orbits ....	68 mm.	32 mm.	40 mm.	....	....
(E) Width across posteriolateral skull corners (greatest skull width) ....	99 mm.	60 mm.	73 mm.	62 mm.	115 mm.
(F) Width across posterior margins of the orbits ....	79 mm.	44 mm.	58 mm.	34 mm.	59 mm.
B/A	0.78	1.18	1.41	0.97	....
D/C	0.86	0.56	0.49	....	....
F/E	0.80	0.73	0.79	0.55	0.52

between eight- and nine-tenths of the length of the skull roof between orbit anterior margins and external nares posterior margins as measured in the midline. In the Spitzbergen and Madagascar genera the width across orbit anterior margins is only about half the length from orbits to external nares.

One feature that may possibly indicate closer relationship of *E. noonkanbahensis* to *A. rostratum* and *W. elongatus* than to *G. kokeni* and *S. nielsenii* concerns the shape of the postorbital portion of the skull. In the Australian, Spitzbergen and Madagascar species the skull increases relatively little in width from the level of the posterior margins of the orbits back to the posterolateral skull corners. In the species from India and Greenland, however, there is marked flaring in the postorbital region. As shown in Table I the width across the posterior margins of the orbits is between seven- and eight-tenths of the width across the skull corners in the first three but only about half in the last two.

#### Comments on stratigraphic correlation and paleoecology

The three fragments of *Erythrobatrachus noonkanbahensis* derive from the upper 10-15 feet of the Blina Shale exposed at V6044. They were found among scree consisting of ferruginized rubble as well as fresh shale fragments. Overlying the Blina Shale slope and about 15 feet above the level on which the fragments were found is a residual rubble of Erskine sandstone. On top of this rubble and capping the hill are remnants of Warrimbah conglomerate. This is the same sequence of rock units as at the Erskine range where the largest collections of fossil vertebrates were acquired. Rough stratigraphic correlation with the Erskine Range

localities is provided by the fact that these lie within the upper 70 feet of the Blina Shale (McKenzie, 1961).

The only other taxon so far identified among fossil material collected at V6044 is a lower jaw fragment of *Deltasaurus kimberleyensis*, U.C.M.P. no. 62158. Material of this animal is abundant at the Erskine Range localities (Cosgriff, 1965) and its presence at V6055 serves to strengthen the stratigraphic correlation of this locality with the Erskine Range localities indicated by the lithologic sequences.

The presence of a slender-skulled, long-snouted trematosaurid in the upper portion of the Blina Shale is consonant with the assignment of this sequence of deposits to the Otoceran division of the Scythian Stage, an assignment based on a variety of paleozoologic and paleobotanic evidence (Cosgriff, 1965 and 1969). Presently available information limits the range of this type of trematosaurid to the lower and middle portions of the Scythian. The range extends from *Erythrobatrachus noonkanbahensis* in the upper part of the Blina Shale which is Otoceran in age to *Aphaneramma rostratum* in the Sticky Keep Formation of Spitzbergen, a unit of Owenitan age (Kummel, 1961). *Stochiosaurus nielsenii* and *Wantzosaurus elongatus* are both Gyronitan in age and, thus, fall in the middle of the range. The former derives from the Wordy Creek Formation of Spitzbergen (Trumpy, 1961) and the latter from the middle portion of the Sakamena Group of Madagascar (see Besaire, 1946 and Lehman, 1961). The stratigraphic positions of these various species relative to each other in Spath's (1935) sequence for the Scythian are shown in table 2. The one trematosaurid of the narrow-skulled, long-snouted group that cannot at present be accurately placed within this sequence is *Gonioglyptus kokeni*

Table 2

Scythian	Stephanitan	
	Columbitan	
	Owenitan	<i>Aphaneramma rostratum</i>
	Flemingitan	
	Gyronitan	<i>Stochiosaurus nielsenii</i> , <i>Wantzosaurus elongatus</i>
	Otocratan	<i>Erythrobatrachus noonkanbahensis</i>

from the *Prionolobus* beds of the Salt Range, India. Kummel and Teichert (1966) have recently investigated the Permian-Triassic sequence in the Salt Range and reviewed the older literature of the subject. As noted by them (*op. cit.*, p. 304), Noetling (1901) included the Zone of *Prionolobus rotundus* in the Ceratite beds of the Salt Range sequence. In their new categorization of the sequence (*op. cit.*, table I, p. 310) the ceratite beds are placed in the Mittiwali Member of the Mianwali Formation and occupy an approximate mid-Scythian position. Thus, although the beds containing *Gonioglyptus kokeni* have not been formally placed in one of Spath's divisions of the Scythian, they are apparently within the stratigraphic range defined by *Erythrosuchus noonkanbahensis* and *Aphaneramma rostratum*.

The possibility of a faunal facies difference existing between the Blina Shale at V6044 and the unit at the Erskine Range localities is suggested by the fact that *Erythrobatrachus noonkanbahensis* is presently known only from the former and has not been identified among a large quantity of fossil vertebrate material collected from the latter. Although such a difference is not substantiated by any lithologic or other faunal distinctions, the nature of occurrences of species related to *E. noonkanbahensis* in other parts of the world provides a suggestion that this may be the case. *Aphaneramma rostratum*, *Gonioglyptus kokeni*, *Stochiosaurus nielsenii* and *Wantzosaurus elongatus* are all associated with marine invertebrates in the deposits in which they occur. This seems to indicate that they were inhabitants of near-shore fresh-water habitats such as deltas, estuaries or lagoons or that they were, indeed, amphibians adapted to an oceanic environment as Wiman (1916) postulated for the family Trematosauridae as a whole. Perhaps, therefore, the Blina Shale at V6044 was deposited in a more seaward area than the Blina Shale at the Erskine Range.

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### 3.—The taxonomic status of small fossil thylacines (Marsupialia, Thylacinidae) from Western Australia

By Jacoba W. J. Lowry\*

With an appendix on statistical methodology by D. R. McNeil†

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Fossil thylacines from the Eucla Division of Western Australia have conspicuously smaller teeth than those of modern *Thylacinus cynocephalus*. With size of teeth the criterion, their taxonomic status is assessed using statistical comparisons that include a test developed by McNeil (see the Appendix). The tests show that for the Eucla Division fossil thylacines, the requirement of the "75 per cent rule" for subspecies is not met at a 95 per cent level of confidence. The Eucla Division fossil thylacines are therefore referred to *Thylacinus cynocephalus*. The re-evaluation of the taxonomic status of fossil thylacines from southwestern Australia, using the same tests, confirms Ride's (1964) conclusion that there is no justification for recognizing these fossils as a new subspecies. However, the heterogeneity of the sample leaves the status of those fossils uncertain. Sexual dimorphism is marked in *Thylacinus* and a statistical method is used to separate some Eucla Division fossil thylacines into presumed males and presumed females.

In the Appendix, McNeil shows that Ride's (1964) method of applying confidence intervals to Mayr's (1969) test for subspecies is invalid. McNeil develops a valid statistical process for testing for subspecies, for both small and large samples.

#### Introduction

During 1966 my husband and I discovered the skeletal remains of eight thylacines (Tasmanian "tigers" or "wolves") in a cave in the Eucla Land Division of Western Australia (Lowry and Lowry, 1967). These, and other fossil vertebrate remains were recovered for the fossil collection of the Geological Survey of Western Australia.

Later examination suggested that the thylacines were very small compared with modern *Thylacinus cynocephalus* from Tasmania, and thus the question arose whether they represented a different species or subspecies. To determine the taxonomic status of specimens from the Eucla Division, I have statistically compared selected dental characters with those of a sample of modern *T. cynocephalus*, and also a sample of fossil thylacines from caves in southwestern Western Australia. Ride (1964) showed that the fossils from southwestern Australia tended to be smaller than *T. cynocephalus*, but he considered them to be conspecific.

During the course of my analysis it appeared that some of the statistical techniques used by Ride (1964) should be re-examined (see the

Appendix), and hence a re-appraisal of the taxonomic status of the southwestern Australian fossils is given here. The analysis led to a consideration of sexual dimorphism in *Thylacinus*, which is discussed at the end of the paper, and a method of determining the sexes in a homogeneous sample is given.

#### The taxonomic assessment of fossil *Thylacinus* samples

##### *Previous taxonomic assessment of fossil Thylacinus*

Only one living species, *Thylacinus cynocephalus* (Harris) from Tasmania, is known. It was common until the beginning of the century, but it is now very rare, possibly extinct. On mainland Australia the genus is represented only by fossils.

Size has been a major criterion in separating the described species. Thus Krefft (1871) described *T. breviceps* from Tasmania as a small species, with larger teeth than *T. cynocephalus*, and Owen (1845) considered *T. spelaeus*, an eastern Australian fossil of the Pleistocene, as simply a larger thylacine than *T. cynocephalus*. Another eastern Australian Pleistocene fossil, *T. rostralis*, was described by De Vis (1894) as also being larger than the living species. The Tertiary fossil *T. potens* Woodburne from Alcoota, central Australia, is even more massive than both *T. spelaeus* and *T. rostralis* (Woodburne, 1967).

Other fossils from mainland Australia are mainly smaller in size than *T. cynocephalus*. The small thylacines from southwestern Australia mentioned above, which Ride (1964) considered conspecific with *T. cynocephalus*, are considered to be of late Quaternary age (Merri- lees, 1968). Apart from the small thylacines recovered by Lowry and Lowry (1967), two further small examples have been recorded from the Eucla Division of Western Australia by Cook (1963) and Partridge (1967), with Partridge's specimen being 3,300 years old. Small fossils have twice been recorded outside Western Australia. A single tooth, 4,000 years old, was found in an excavation in a rock shelter at Fromms Landing, South Australia (Macintosh and Mahoney, 1964), and a small thylacine is known from Lake Menindee, New South Wales (Woodburne, 1967).

\*Honorary Associate, Western Australian Museum, Beaufort Street, Perth 6000.

†Statistics Department, Princeton University, New Jersey, U.S.A.



### *Size as a taxonomic criterion in Thylacinus*

Previous workers have mostly used size as a criterion for distinguishing thylacine species, and the present study therefore is limited to a consideration of size. The size of an individual thylacine depends in part on its maturity, a problem avoided by measuring and analysing selected tooth dimensions, assumed to remain constant throughout an individual's life. This choice is important because the individuals in the Eucla Division sample show a great range in maturity. Furthermore, post-cranial remains are relatively scarce in the southwestern Australian sample, and no data on post-cranial remains of modern *T. cynocephalus* were available.

There appear to be certain short-comings in some of the previous analyses of size differences between thylacines from various localities. The species concept of the early taxonomists, even if not classically "typological", did not emphasize interbreeding populations and reproductive isolation, as does the "biological" or "evolutionary" concept prominent today (Mayr, 1969), and a concept of a range of variation within a given species was often neglected. For example, *T. breviceps* was based on a sample of two specimens, and both *T. rostralis* De Vis and *T. breviceps* Krefft were compared with a single specimen of *T. cynocephalus*. As neither De Vis (1894) nor Krefft (1871) identify the specimen, it is not known if the same one was used on both occasions. Not surprisingly the validity of some of the species erected during that period has been questioned. Thus Stephenson (1963) considered that *spelaeus* should lapse into synonymy because he considered the differences in size between *T. spelaeus* and *T. cynocephalus* were negligible. This was demonstrated by Ride (1964), who showed that there was no statistically significant difference between mean values of selected dental characters. The short-comings mentioned above can be reduced by taking large samples and analysing them statistically because "the erection of a taxonomic subspecies, species or genus by inferring the nature and limits of corresponding morphological groups from a series of given specimens is essentially a statistical problem" (Simpson, 1943).

Since natural populations of sexually reproducing animals can be expected to differ from one area to another, it is not enough to simply find statistically significant differences between populations to establish a new species or subspecies (Mayr, 1969). The problem of intra-specific variation is more acute when a time element is introduced. The early workers on *Thylacinus* do not seem to have considered the possibility of intra-specific evolutionary changes involving body size, yet during the Quaternary many mammals have shown fluctuations in size (Hooijer, 1949; Kurtén, 1964, 1965, 1968), including much post-Pleistocene dwarfing. Because a short time is involved, Hooijer and Kurtén believed that the differences between the large Pleistocene forms and some of the smaller modern forms are often no more than subspecific. Thus size as a criterion for distinguishing between species of Quaternary mammals

should be used with caution. The Quaternary fossil thylacines may in fact have represented populations of larger and smaller individuals of a single species, that existed on the mainland at different periods of time. Ride (1964) claimed that differences between the small sized southwestern Australian fossils and *T. cynocephalus* were not great enough to warrant even subspecific recognition, but since the Eucla Division fossils appear to be even smaller, the possibility that they represented a subspecies of *T. cynocephalus*, rather than a new species, is considered.

### *The recognition of subspecies in small samples*

Although the species category has objective reality (Simpson, 1943) the subspecies, like the higher categories, has subjective boundaries (Simpson, 1943; Amadon, 1949; Mayr, 1969). The subspecies category has been defined by Mayr (1969) as "an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of the species, and differing taxonomically from other populations of the species". Where there are clear-cut differences between two such populations, the recognition of subspecies is quite simple, but where their intra-population range of variation overlap, a "75 per cent rule" is often used to determine if enough difference exists to warrant recognition by name (Amadon, 1949). This rule or convention is subject to various interpretations, but it is usually required that 75 per cent of specimens in a sample from the proposed new subspecies must differ from "all" (97 to 99 per cent) specimens from all other previously recognised subspecies (Amadon, 1949; Mayr, 1969). The requirement of the rule is approximately met when 90 per cent (or more) is separable from 90 per cent (or more) of samples of all previously recognised subspecies (Mayr, 1969). It is also easier to calculate percentage separation when overlap is symmetrical.

The statistic Coefficient of Difference (abbreviated to CD) proposed by Mayr (1943) and discussed by Mayr (1969) attempts to show whether the requirement of the 75 per cent rule has been met. It is based on the observation that the degree of overlap of two curves is related to the difference of their mean divided by the sum of their standard deviations. With the aid of a table, CD can be used to show whether two samples are sufficiently separate for the populations they represent to be arbitrarily accorded subspecies status. Mayr (1969) gives a table of values of CD and the corresponding percentage separation. See also Table I in the Appendix by McNeil.

The advantage of CD is its simplicity and ease of calculation, but the statistic assumes that the populations are normally distributed, and that values of sample statistics equal those of population parameters; hence calculated values of CD can at best only give an indication of magnitude of overlap between two curves. In borderline cases, or where these assumptions cannot be made, such as when samples are small, a more accurate test is required.



Different authors require different values of CD to demonstrate subspecific separation, depending on their interpretation of the 75 per cent rule. Thus Mayr (1969) requires a value of at least 1.28, representing a separation of at least 90 per cent from 90 per cent, but others are more stringent, requiring up to 97 per cent separable from 97 per cent (Amadon, 1949), which is indicated by a CD value of 1.9. In his study of *Thylacinus*, Ride (1964) considered an intermediate value for CD of 1.5, representing a separation of about 94 per cent from 94 per cent, as adequate for the recognition of subspecies, but that a more stringent test should apply when samples are small, as were the fossil samples available to him. He therefore modified the statistic Coefficient of Difference as given by Mayr and others (1953) by calculating its 95 per cent confidence interval, and requiring a value of at least 1.5 for the lower limit.

Since this paper is in part a continuation and re-evaluation of Ride's (1964) work on *Thylacinus*, it seemed appropriate to extend his statistical approach to the analysis of the Eucla Division thylacines, and to require a value greater than 1.5 for lower confidence limits, when testing percentage separation of the fossils from *T. cynocephalus*. However, McNeil (see the Appendix) shows that Ride's (1964) modification is invalid, and gives the mathematical development of an accurate statistic to which confidence intervals can be applied. I therefore use this statistic and confidence interval, but follow Ride (1964) by requiring a value greater than 1.5 for the lower confidence limit to indicate adequate separation of samples to warrant subspecies recognition of the populations they represented. The 95 per cent confidence interval applied to the statistic developed by McNeil does not give as wide an interval as the one used by Ride (1964); hence I re-evaluate the taxonomic status of the southwestern Australian fossil thylacines. Also, a few more fossil specimens have been discovered since the publication of Ride's (1964) paper.

#### *The use of normal statistics with samples of Thylacinus.*

*Thylacinus cynocephalus* from Tasmania shows strong sexual dimorphism, with males tending to have larger teeth than females (Ride, 1964). Thus the distribution of dental characters from samples of *T. cynocephalus* tend to be bimodal. I have therefore applied  $\chi^2$  tests to the data from the sample of modern Tasmanian thylacines (the only one large enough for the meaningful use of this test), to check whether frequency distributions depart statistically significantly from normality, thus rendering tests based on this assumption invalid. The  $\chi^2$  probabilities are not significant, except for the length of the upper 2nd molar ( $M^2$ ) and the length of the lower 4th molar ( $M_4$ ). Hence results for these characters are doubtful.

#### **Description of the *Thylacinus* samples.**

##### *The control sample of modern Thylacinus cynocephalus from Tasmania*

Dr. W. D. L. Ride (Director, Western Australian Museum) has kindly made available to me many data (largely unpublished) on modern *T. cynocephalus*. These specimens are now lodged at widely separate institutions (see Ride, 1964), which prevented me from re-measuring them. To test my ability to reproduce Ride's measurements I re-measured those fossils in the Western Australian Museum originally measured by him, and applied a t-test (Simpson and others, 1960) to these paired data. The probability that my measurements and Ride's were the same ranged from greater than 50 per cent to greater than 70 per cent. Tooth dimensions are recorded to 0.1 mm, and since 0.1 mm amounts to only one or two per cent of the dimensions of the tooth measurements, I therefore consider comparisons of Ride's data with mine to be valid. Ride (1964) selected the data he published to exclude measurements from juveniles because some of the characters he used include bone and thus are affected by growth, but since I analyse only dental characters, I have included measurements from juveniles. Hence the values for calculated statistics that Ride (1964) records in his Tables 1 and 2 for the four dental characters I also use ( $M^2$ ,  $M^3$ ,  $M_4$ , and  $P_4$ ), are not precisely the same as the values I record in this paper.

##### *The Eucla Division fossil Thylacinus sample*

All fossil thylacines from the Eucla Division were found on the surface of the floors of caves (see figure 1 for the location of the caves). Cave numbers (e.g. N63 below) are those of the cave registration system of the Australian Speleological Federation. Specimen catalogue numbers like 64.8.1 refer to the fossil collection of the Western Australian Museum, and those like F6358 refer to fossils from the collection of the Geological Survey of Western Australia at present housed in the Western Australian Museum.

##### (i) From Thylacine Hole (N63)

Thylacine Hole (31° 42' S; 127° 44' E) is about 100 km west of Eucla, and lies on the Hampton Tableland, a semi-arid region characterised by grassy flats and tree-covered ridges. The cave has been described by Lowry and Lowry (1967) who recovered partial or complete skeletons representing eight different thylacines. One of them, F6364, is a remarkably preserved carcass, from which hair and soft tissue has been dated (NSW 28c) at  $4,650 \pm 153$  years BP (Lowry and Merrilees, 1969; Merrilees, 1970). Five specimens, F6353, F6354, F6355, F6357 and F6358, are nearly complete skeletons that include measureable teeth. One specimen, F6356, does not include teeth, and another, F6360, consists only of the pelvis and part of the vertebral column. Measurements from the carcass F6364 are not included in the statistical sample because they could not be made accurately without damaging the specimen.

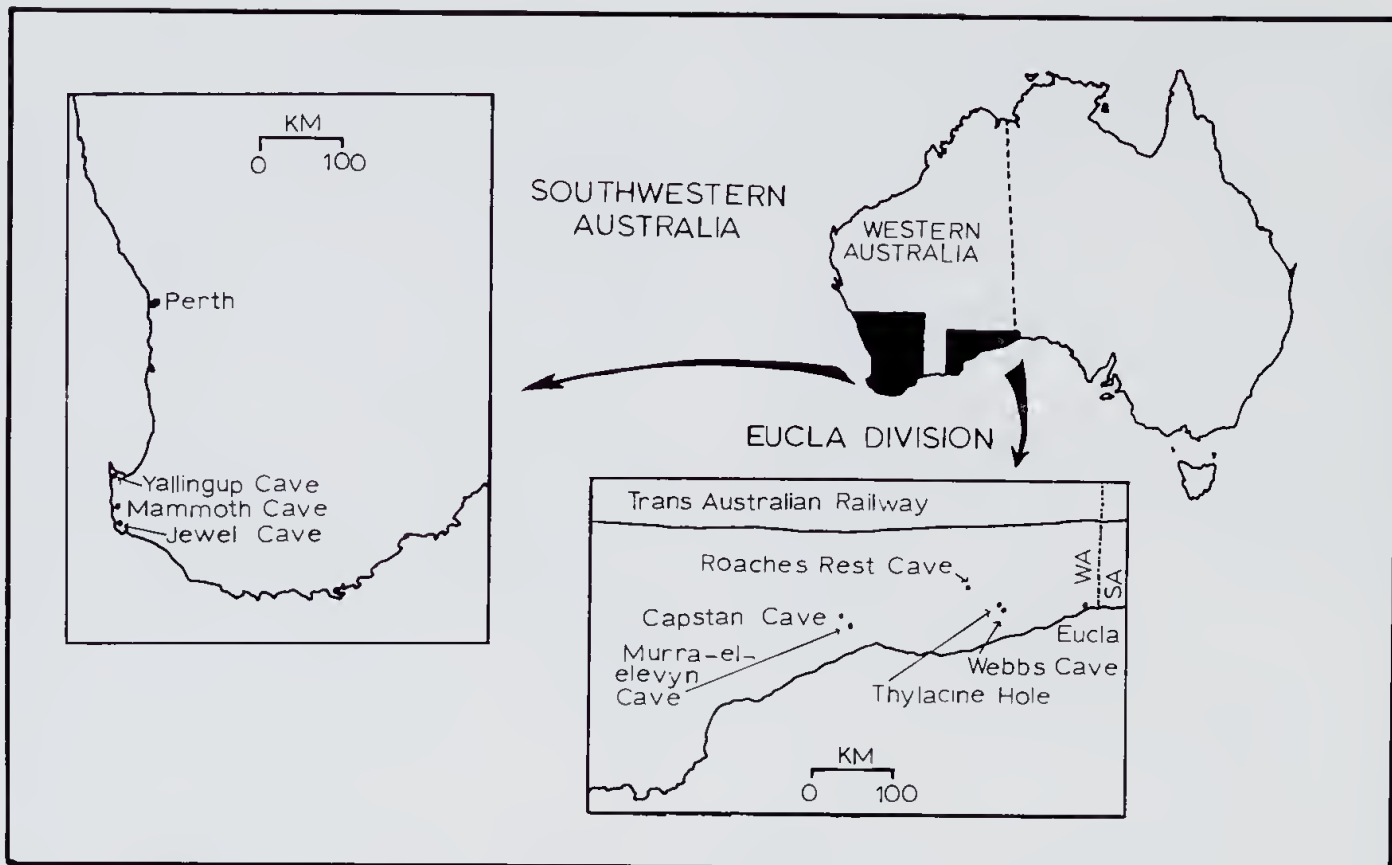


Figure 1.—Locality maps.

The remains represented animals in their death positions, except F6360 which had been disturbed by water wash. All had probably fallen nearly 12 metres through the sole narrow chimney-like entrance into the cave, yet only one specimen, F6355, has broken bones, and even this may have occurred after death through roof collapse of the cave. F6358 is a juvenile with the basioccipital—basipresphenoid and basipresphenoid—presphenoid sutures open, the upper fourth molars not erupted, and no perceptible wear on the teeth. In F6357 both these sutures are fused and the teeth are well worn. The other three specimens show intermediate stages of maturity.

(ii) From Murra-el-elevyn Cave (N47)

Murra-el-elevyn Cave ( $32^{\circ} 03' S$ ;  $126^{\circ} 02' E$ ) is about 6.4 km west of Cocklebiddy Motel, on the Hampton Tableland. A single specimen, 64.8.1, with adhering soft tissue dated (GaK 693)  $3,280 \pm 90$  years BP (Partridge, 1967) was recovered from the cave. All teeth are present.

(iii) From Roaches Rest Cave (N58)

Roaches Rest Cave ( $31^{\circ} 33' S$ ;  $127^{\circ} 14' E$ ) is about 45 km northwest of Madura, and lies on the tree-less Nullarbor Plain *sensu stricto*. The single specimen, 67.3.21, represented a juvenile, and consists of fragments of the lower jaw and skull. Some teeth are missing and others are not measurable.

(iv) From Capstan Cave (N50)

Capstan Cave ( $32^{\circ} 01' S$ ;  $125^{\circ} 57' E$ ) is about 14.5 km west of Cocklebiddy Motel, on the Nullarbor Plain. The single specimen, 67.11.37, is a right dentary, and carries measurable first and third premolar and first molar teeth.

(v) From Webbs Cave (N132)

Webbs Cave ( $31^{\circ} 46' S$ ;  $127^{\circ} 50' E$ ) lies on the Hampton Tableland, and is near Thylacine Hole, about 90 km west of Eucla. Cook (1963) described a single upper molar, 70.7.54, from this cave. The specimen is mentioned again below, but is not included in my statistical sample because its position in the tooth row is not known with certainty.

*The southwestern Australian fossil Thylacinus sample*

The fossil sample from the southwest of Western Australia includes all specimens measured by Ride (1964, "Western Cave-fossil *Thylacinus*") and those discovered subsequently. Thus the values of calculated statistics I give in Tables 1, 2, and 3 for the dental characters  $M^2$ ,  $M^3$ ,  $M_4$  and  $P_4$  are not precisely the same as those recorded by Ride (1964). Most of the specimens came from caves formed in Quaternary eolianite in the extreme southwestern portion of Western Australia (Figure 1), such as Yallingup Cave (Ya 1), Mammoth Cave (Wi 38-39), and Jewel Cave (Au 13). Two specimens, 61.2.19-23 and 63.7.7, came from caves about 100 km north of Perth. Three of the specimens from the extreme southwest, 61.2.26, 61.2.27, and 61.2.28, came from Mammoth Cave, from a deposit which appears to be more than 37,000 years old (Lundelius, 1960; Merrilees, 1968). Merrilees (1968) considers these to be the oldest specimens available from Western Australia, but that even these are unlikely to be older than late Quaternary.



# Statistical assessment of Western Australian fossil *Thylacinus*

## Results and discussion of statistical tests

The statistical procedure I use to determine the taxonomic status of the fossil samples is similar to the one advocated by Ride (1964, Appendix). After applying  $\chi^2$  tests to check the normality of the data and F-tests to check that sample variances do not differ significantly, mean dimensions of dental characters are compared using a standard t-test. Those characters that give statistically significant values for t are tested for subspecies separation using the statistic developed by McNeil (see the Appendix). A value greater than 1.5 for the lower confidence limit is required to establish subspecies status.

The following dental characters were measured and tested. I follow Ride (1964) in nomenclature.

- (i) Upper molars 1 to 3 ( $M^1$  to  $M^3$ )—diagonal length through protocone to metacone.
- (ii) Lower molars 1 to 4 ( $M_1$  to  $M_4$ )—length.
- (iii) Lower premolars 1, 3, and 4 ( $P_1$ ,  $P_3$  and  $P_4$ )—length.

Upper molars were measured along the longest diagonal crossing the protocone and metacone, and lower molars and premolars along the greatest length in an approximately antero-posterior direction. For consistency right teeth were chosen where possible, although they tend to be a little larger than teeth from the left side. This difference is not significant however. Of 153 pairs of measurements, the mean value of measurements from the right side is 10.21 mm and from the left side 10.18 mm. Copies of the raw data, together with an explanation of their

meaning and accuracy have been lodged in the libraries of the University of Tasmania, Hobart, and the Western Australian Museum, Perth.

Table 1 gives a summary of the dimensions of the dental characters tested, and shows that teeth from the Eucla Division fossils are generally smaller than those of the southwestern Australian fossils, and conspicuously smaller than those of modern *Thylacinus cynocephalus*. Standard tests of comparison were applied to all the data, despite the questionable normality of the lengths of  $M^2$  and  $M_1$  from the modern *T. cynocephalus* sample. Table 2 shows that results of standard tests applied to data from these two characters follow the same trends as those shown by the other characters, and hence can probably be accepted.

Results of F-tests are given in Table 2, and show that the sample variances generally do not differ between the three thylacine samples, excepting variances for the dimensions of  $P_4$  and  $M_3$  from the southwestern Australian fossils. Since in practice the t-test is a robust test (Simpson and others, 1960) it was also applied to these two characters.

Results of the t-tests are given in Table 2, and show that there is no statistically significant difference between mean dimensions of dental characters of the southwestern Australian and Eucla Division fossils at the one per cent level. All the tests between fossil samples and modern *T. cynocephalus* gave significant results at the one per cent level, except the mean dimension of the length of  $P_1$  of the Eucla Division fossils. It is therefore worth testing whether the requirement of the 75 per cent rule for subspecies is met.

Table 1

Summary of dimensions of dental characters of the *Thylacinus* samples.

Character†	Modern <i>Thylacinus cynocephalus</i>					Southwestern Australian Fossil <i>Thylacinus</i>					Eucla Division Fossil <i>Thylacinus</i>				
	Mean $\bar{X}$ mm.	Observed Range mm.	n	s mm.	V	Mean $\bar{X}$ mm.	Observed Range mm.	n	s mm.	V‡	Mean $\bar{X}$ mm.	Observed Range mm.	n	s mm.	V‡
$M^1$ ....	11.6	10.1–12.7 (2.6)	60	0.61	5.3	10.3	9.5–12.1 (2.6)	12	0.72	7.2	10.2	9.5–11.0 (1.5)	7	0.52	5.3
$M^2$ ....	15.1	13.6–16.6 (3.0)	61	0.88	5.8	13.0	11.4–15.9 (4.5)	12	1.06	8.4	12.5	11.2–13.2 (2.0)	6	0.72	6.1
$M^3$ ....	17.8	15.4–20.2 (4.8)	54	1.23	6.9	15.4	13.1–17.7 (4.6)	9	1.25	8.4	14.6	13.7–15.3 (1.6)	6	0.77	5.5
$P_1$ ....	6.2	5.3–7.0 (1.7)	63	0.42	6.9	5.6	4.9–6.4 (1.5)	9	0.49	9.0	5.9	5.5–6.3 (0.8)	6	0.31	5.6
$P_3$ ....	9.2	8.1–10.1 (2.0)	64	0.46	5.0	8.1	7.1–9.1 (2.0)	11	0.66	8.4	7.8	7.0–8.3 (1.3)	7	0.50	6.6
$P_4$ ....	10.8	9.2–11.9 (2.7)	64	0.59	5.4	10.0	8.7–12.1 (3.4)	13	1.05	10.7	9.7	8.9–11.0 (2.1)	6	0.82	8.8
$M_1$ ....	9.6	8.6–10.6 (2.0)	39	0.57	6.0	8.6	7.5–9.8 (2.3)	13	0.66	7.8	8.3	7.9–9.0 (1.1)	7	0.45	5.6
$M_2$ ....	11.9	11.0–13.2 (2.2)	41	0.53	4.5	11.2	10.2–12.6 (2.4)	11	0.75	6.8	10.4	9.9–11.2 (1.3)	8	0.48	4.7
$M_3$ ....	14.1	12.8–15.3 (2.5)	41	0.57	4.1	13.0	11.1–15.0 (3.9)	12	1.18	9.3	12.3	11.5–13.0 (1.5)	7	0.67	5.7
$M_4$ ....	15.8	13.9–17.2 (3.3)	53	0.92	5.8	14.5	12.8–16.9 (4.1)	12	1.32	9.3	13.5	11.8–14.2 (2.4)	6	0.95	7.3

† Characters are described in the text on page 23.

‡ Coefficient of Variation corrected for small sample size using a correction developed by Haldane (1955).

Table 2

Results of standard tests of comparison.

Character†	Modern <i>Thylacinus cynocephalus</i> compared with Eucla Division fossil <i>Thylacinus</i>			Modern <i>Thylacinus cynocephalus</i> compared with southwestern Australian <i>Thylacinus</i>			Southwestern Australian fossil <i>Thylacinus</i> compared with Eucla Division fossil <i>Thylacinus</i>		
	Variance		Mean	Variance		Mean	Variance		Mean
	F	p		F	p		F	p	
M <sup>1</sup>	1.38	>0.2	<0.001**	1.40	>0.2	<0.001**	1.93	>0.2	0.8>x>0.7
M <sup>2</sup>	1.47	>0.2	<0.001**	1.46	>0.2	<0.001**	2.14	>0.2	0.3>x>0.2
M <sup>3</sup>	2.55	>0.2	<0.001**	1.04	>0.2	<0.001**	2.66	>0.2	0.3>x>0.2
P <sub>1</sub>	1.83	>0.2	0.2>x>0.1	1.34	>0.2	<0.001**	2.45	>0.2	0.3>x>0.2
P <sub>2</sub>	1.18	>0.2	<0.001**	2.02	0.1>x>0.05	0.01<x<0.001**	1.75	>0.2	0.5>x>0.4
P <sub>3</sub>	1.94	>0.2	<0.001**	3.20	<0.01**	<0.001**	1.64	>0.2	0.6>x>0.5
M <sub>1</sub>	1.61	>0.2	<0.001**	1.34	>0.2	<0.001**	2.15	>0.2	0.3
M <sub>2</sub>	1.24	>0.2	<0.001**	1.99	0.2>x>0.1	<0.001**	2.47	0.2>x>0.1	0.02>x>0.01*
M <sub>3</sub>	1.36	>0.2	<0.001**	4.26	<0.01**	<0.001**	3.13	>0.2	0.2>x>0.1
M <sub>1</sub>	1.07	>0.2	<0.001**	2.03	0.2>x>0.1	<0.001**	1.93	>0.2	0.2>x>0.1

† Characters are described in the test on page 23.

\* Significant at the 5 per cent level.

\*\* Significant at the 1 per cent level.

Results of the test developed by McNeil (see the Appendix) are given in Table 3, and show that no characters from the south-western Australian fossils achieve a significant value of greater than 1.5. Thus the use of a more accurate statistic, a larger sample, and the consideration of extra characters, does not alter Ride's (1964) conclusion that the southwestern Australian fossils are insufficiently separate from *T. cynocephalus* to warrant the creation of a new subspecies, let alone a new species.

The requirement of the 75 per cent rule is met in two dental characters (M<sup>2</sup> and M<sub>3</sub>) from the Eucla Division fossil thylacines, but none of the lower 95 per cent confidence limits achieve this level of significance. Hence one cannot be sure that 94 per cent of the dimensions of these two characters will be separable from 94 per cent of those from modern *T. cynocephalus* in 95 per cent of all possible samples that might be taken from both populations. Since the data from modern *T. cynocephalus* on the length of M<sup>2</sup> is of questionable normality, the result of the test for this character would have been interpreted with caution, even if the lower confidence limit had achieved a statistically significant value. Accordingly, although the teeth of the Eucla Division fossils are significantly smaller, this is an inadequate reason for separating them from *Thylacinus cynocephalus*.

Although the criterion of mean size indicates that the southwestern Australian fossil thylacines should be referred to *T. cynocephalus*, their status is not clear because of the heterogeneity of the sample. This is demonstrated by a high Coefficient of Variation (V) and also a large observed range of variation (Table 1). The mean dimensions given in Table 1 mask the fact that there are four individual specimens from the southwestern Australian sample with tooth dimensions exceeding the mean values of the modern *T. cynocephalus* sample, and that there are five individual specimens with tooth dimensions below the mean values of the Eucla Division sample. Two of the large specimens came from Mammoth Cave, and thus are probably late Pleistocene in age (see above). Until more specimens that can be dated are found from both the southwest of Western Australia and the Eucla Division, there is no way of deciding between three alternatives:—(1) there were two species, a smaller and a larger in southwestern Australia; (2) the size range illustrates an intra-specific post-Pleistocene trend to size reduction in *Thylacinus* in southwestern Australia, as seen in some other mammals (see above); (3) the southwestern Australian fossil thylacines were simply more variable than other populations.

#### The taxonomic status of the thylacine tooth from Webbs Cave (N132)

The Webbs Cave tooth, 70.754, was not included in the Eucla Division statistical sample because the position in the tooth row of an isolated tooth is difficult to determine with certainty, but Cook (1963) is probably correct in calling it a left upper 3rd molar. The tooth has a length of 12.8 mm, which is considerably smaller than the mean dimension of 14.6 mm for upper 3rd molars from the Eucla Division sample, but a t-test gives a probability of just



over 5 per cent that it could have come from the Eucla Division population. I therefore refer this molar, assuming it to be an upper 3rd molar, to the Eucla Division fossil thylacines, and hence to *T. cynocephalus*.

#### Sexual dimorphism in *Thylacinus*

Modern *T. cynocephalus*, as mentioned above, shows strong sexual dimorphism. Ride (1964) showed that tooth dimensions of modern thylacines of known sex tend to fall into two groups, with those of males being larger than those of females. Thus where the sex of an individual specimen is unknown, its possible sex could be determined by comparing its tooth dimensions with those from other specimens from the same population.

**Table 3**  
*Test for subspecies*

Character†	Southwestern Australian Fossil <i>Thylacinus</i>		Eucla Division Fossil <i>Thylacinus</i>	
	CD	CD <sub>1</sub> *	CD	CD <sub>1</sub> *
M <sup>1</sup> ....	0.97	0.68	1.11	0.74
M <sup>2</sup> ....	1.16	0.85	1.51*	1.10
M <sup>3</sup> ....	1.00	0.67	1.33	0.93
P <sub>1</sub> ....	0.61	0.31	0.33	—0.02
P <sub>3</sub> ....	1.14	0.83	1.46	1.07
P <sub>4</sub> ....	0.53	0.30	0.86	0.49
M <sub>1</sub> ....	0.83	0.54	1.16	0.78
M <sub>2</sub> ....	0.59	0.30	1.48	1.07
M <sub>3</sub> ....	0.75	0.45	1.59*	1.16
M <sub>4</sub> ....	0.66	0.38	1.26	0.85

† Characters are described in the text on page 23.

\* Significant result.

**Table 4**  
*Determination of sex in fossil Thylacinus from Thylacine Hole*

Specimen Numbers	Ranks*					Score†
	1 (smallest)	2	3	4	5 (largest)	
F6358 ....	5	3	1	....	....	14
F6354 ....	4	4	1	....	....	15
F6353 ....	....	....	3	5	1	34
F6355 ....	....	....	3	4	2	35
F6357 ....	1	1	1	3	3	33

\* Rank columns record the frequency with which characters from each specimen were accorded a particular rank.

† Score column records the sum of the products of the ranks and frequencies for each specimen, and is a numerical expression of the visual assessment of its size, relative to the other specimens.

As with modern *T. cynocephalus*, the tooth dimensions of five specimens from Thylacine Hole also tend to fall into two groups, which could represent sexes. The following method considered all ten measured characters simultaneously in establishing the grouping of the fossils. Dimensions of dental characters were ranked from 1 (smallest) to 5 (largest) and the "rank" columns in Table 4 record the frequency with which the dimensions of characters from each specimen were accorded a particular rank. The "score" column in Table 4 records the sum of the products of the ranks and frequencies, for each specimen. For example, F6358 ranked smallest for the dimensions of 5 characters, second smallest for the dimensions of 3 characters and third in size for one character, and has a score of  $5 \times 1 + 3 \times 2 + 1 \times 3 = 14$ . This is a numerical expression of the visual observation that its teeth are the smallest of the five Thylacine Hole fossils. Table 4 records two specimens with small teeth (scores under 20) and three with large teeth (scores over 30). I suggest this grouping represents females and male respectively, from a population that on the whole had smaller teeth than the modern Tasmanian thylacine population.

It is possible to argue that the fossils from Thylacine Hole represented two species, one with smaller teeth than the other, but this seems unlikely because modern *Thylacinus* is known to show strong sexual dimorphism (Ride, 1964), and also, the pattern obtained by ranking the dimensions of their teeth indicates that the ratios of tooth measurements within an individual specimen are similar for each of the specimens. A concept of two sexes in a single species is more consistent with this observation than one of two species that lived in the area.

The best preserved fossil thylacine specimen from Thylacine Hole, F6364, was not included in Table 4 because only a few of its teeth could be measured without damaging the desiccated vibrissae, tongue and lips, but I have "ranked and scored" those measurements available from F6364 with corresponding measurements from the other tooth-bearing Thylacine Hole specimens. Its score groups with the two presumed females, and so the carcass probably represented a female.

The determination of the possible sex of an isolated specimen is more complex because thylacine samples from various places on the Australian mainland all have teeth of different mean dimensions. Thus the suggestion by Partridge (1967), that the specimen from Murra-el-elevyn Cave, 64.8.1 might have represented a female on the basis of its small teeth when compared with mean values for dental characters from the southwestern Australian fossils, cannot now be supported. Subsequent discoveries have shown that the teeth of all thylacines known from the Eucla Division tend to be smaller than mean values for teeth from the southwestern Australian fossils. Furthermore, the method described above apparently can only be used with specimens from the same local population. When tooth dimensions of 64.8.1 are "ranked and scored" with the five

Thylacine Hole specimens, its score is found to lie exactly between those of the presumed males and females, and thus its sex remains uncertain.

Similarly, the sex of the thylacine represented by 70.7.54, the Webbs Cave tooth (Cook, 1963), cannot be determined with certainty because dimensions of several characters from the one specimen need to be assessed simultaneously during the comparisons. However, assuming that the tooth is an M<sup>3</sup>, it is the smallest I have measured, and hence may have represented a female, as suggested by Cook (1963).

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#### Appendix: Statistical Methodology for Subspecific Separation of Two Populations

By D. R. McNeil

##### The Coefficient of Difference

Suppose we have two populations of individuals, and  $X$  is a characteristic (such as the height of an individual). Let  $X_1$  and  $X_2$  represent the characteristics for individuals from the first and second population, respectively. Suppose also that  $X_1$  and  $X_2$  are normally distributed random variables, with expectations  $\mu_1$ ,  $\mu_2$  and variances  $\sigma_1^2$ ,  $\sigma_2^2$ , respectively. Put

$$(1) \quad F_i(x) = \text{Probability that } X_i \leq x, i = 1, 2.$$

Then  $F_i(x)$  is the probability that the characteristic of an individual chosen at random from population  $i$  will not exceed  $x$ .  $F_i(x)$  is called the cumulative probability distribution of  $X_i$ , and may be written

$$(2) \quad F_i(x) = \int_{-\infty}^x f_i(z) dz, i = 1, 2,$$

where  $f_i(z)$  is the normal probability density function, i.e.

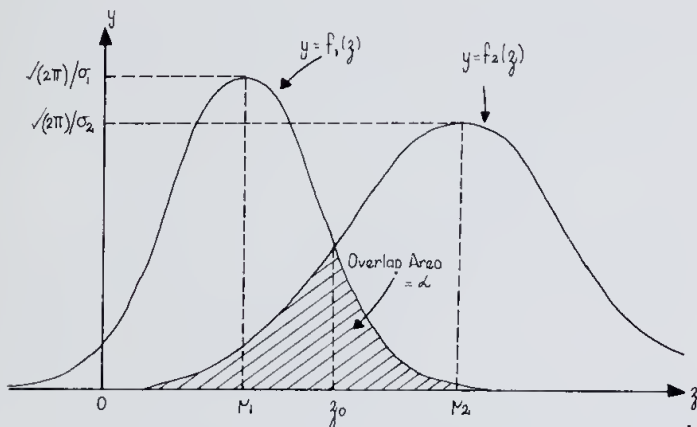
$$(3) \quad f_i(z) = (2\pi\sigma_i^2)^{-1/2} \exp\left\{-\frac{1}{2}\left(\frac{z - \mu_i}{\sigma_i}\right)^2\right\}, i = 1, 2.$$

The graphs of  $f_1(z)$  and  $f_2(z)$  are depicted in Figure 1.

If one is interested in measuring the difference between the two populations on the basis



of the characteristic  $X$ , a suitable measure must be defined. For definiteness let us assume that  $\mu_2 > \mu_1$ .



Appendix Figure 1.—Curves of the probability densities of the characteristic  $X$ , for the two populations, the variances  $(\sigma_1^2$  and  $\sigma_2^2)$  being unequal.

One such measure is  $\mu_2 - \mu_1$ , the difference in the expectations of  $X$  for the two populations. Another is the *proportion of overlap* between the two populations, defined as the shaded area in Appendix Figure 1. If  $z_0$  is the point at which the two curves intersect, then the proportion of overlap is obtainable by integration as

$$\begin{aligned} \alpha &= \int_{-\infty}^{z_0} f_2(z) dz + \int_{z_0}^{\infty} f_1(z) dz, \\ (4) \quad &= F_2(z_0) + 1 - F_1(z_0). \end{aligned}$$

A third measure of the difference between the two populations is the *coefficient of difference*

$$(5) \quad CD = \frac{\mu_2 - \mu_1}{\sigma_1 + \sigma_2},$$

which is commonly used in zoology (see, for example, Mayr, 1969, p. 189).

If the two populations have the same variance, then  $\sigma_1 = \sigma_2 = \sigma$ , say, and, using (3),  $z_0$  is given by the (necessarily unique) point where the curves intersect.

Putting  $f_1(z_0) = f_2(z_0)$  we get

$$\begin{aligned} (2\pi\sigma^2)^{-1/2} \exp\left\{-\frac{1}{2}\left(\frac{z_0 - \mu_1}{\sigma}\right)^2\right\} \\ = (2\pi\sigma^2)^{-1/2} \exp\left\{-\frac{1}{2}\left(\frac{z_0 - \mu_2}{\sigma}\right)^2\right\}. \end{aligned}$$

Solving for  $z_0$  we get  $(z_0 - \mu_1)^2 = (z_0 - \mu_2)^2$ , so that  $z_0 = \frac{1}{2}(\mu_1 + \mu_2)$ . Putting this in (4), we find

$$\begin{aligned} (6) \quad \alpha &= \int_{-\infty}^{\frac{1}{2}(\mu_1 + \mu_2)} (2\pi\sigma^2)^{-1/2} e^{-\frac{1}{2}(z - \mu_2)^2/\sigma^2} dz \\ &+ 1 - \int_{-\infty}^{\frac{1}{2}(\mu_1 + \mu_2)} (2\pi\sigma^2)^{-1/2} e^{-\frac{1}{2}(z - \mu_1)^2/\sigma^2} dz. \end{aligned}$$

The right-hand side of equation (6) may be reduced after some simplification to

$$(7) \quad \alpha = 2\Phi\left(-\frac{\mu_2 - \mu_1}{2\sigma}\right),$$

where  $\Phi(x)$  is the standardized normal cumulative distribution function, i.e.,

$$\Phi(x) = \int_{-\infty}^x (2\pi)^{-1/2} \exp\left(-\frac{1}{2}z^2\right) dz.$$

But in the case  $\sigma_1 = \sigma_2 = \sigma$ , the coefficient of difference is, using (5),

$$(8) \quad CD = \frac{\mu_2 - \mu_1}{2\sigma},$$

so that when the variances of the two populations are equal, the proportion of overlap and the coefficient of difference are related by the formula

$$(9) \quad \alpha = 2\Phi(-CD).$$

It may be noted that as  $CD$  increases from 0 to  $\infty$ ,  $\alpha$  decreases from 1 to 0. (This can be seen by inspection of Figure 1.) Thus, the larger the value of the coefficient of difference, the smaller the proportion of overlap between the two populations. Some values of  $\alpha$  corresponding to various values of  $CD$  are given in Appendix Table 1. Thus a value of  $CD = 1$  corresponds to a 32% overlap, that is, 16% of the first population are indistinguishable from 16% of the second. A value of  $CD = 2$  corresponds to only 2.3% of the first population being indistinguishable from 2.3% of the second. A discussion of the relationship between  $\alpha$  and  $CD$  is also given by Mayr (1969, p. 190).

#### Description of Ride's Method

In order to determine whether or not two populations are sufficiently different to warrant separate classification, zoologists have suggested that the  $CD$  be used as a measure, but have disagreed on the value required. In practice, it is not possible to measure  $CD$  exactly, since one usually has only a small sample of observations of  $X_1$  and  $X_2$ , and consequently any estimates of  $CD$  will be subject to sampling error. In a situation like this it is customary to obtain a confidence interval for  $CD$ . Such an interval can then be said to contain  $CD$  with a specified degree of certainty (usually 95%). If the interval obtained is wholly above the minimum value

Appendix Table 1

Values of the proportion of overlay,  $\alpha$ , corresponding to the coefficient of difference,  $CD$ .

$CD$ ....	....	....	0.50	1.00	1.25	1.50	1.75	2.00	2.25	2.50	2.75	3.00
$\alpha$ ....	....	....	0.62	0.32	0.21	0.13	0.08	0.046	0.024	0.012	0.006	0.002

of CD which is sufficient for separate classification of the populations, then one can say that that the populations are separate.

The problem of obtaining a confidence interval for the coefficient of difference has already been considered by Ride (1964), who gives as a 95% confidence interval ( $CD_1$ ,  $CD_2$ ), where

$$CD_1 = \frac{[\bar{x}_2 - t_2 s_2 n_2^{-1/2}] - [\bar{x}_1 + t_1 s_1 n_1^{-1/2}]}{[(n_1 - 1)^{1/2} s_1 / \chi_{11}] + [(n_2 - 1)^{1/2} s_2 / \chi_{21}]},$$

$$CD_2 = \frac{[\bar{x}_2 + t_2 s_2 n_2^{-1/2}] - [\bar{x}_1 - t_1 s_1 n_1^{-1/2}]}{[(n_1 - 1)^{1/2} s_1 / \chi_{12}] + [(n_2 - 1)^{1/2} s_2 / \chi_{22}]},$$

and:

$\bar{x}_1$  and  $\bar{x}_2$  are the two sample means

$s_1^2$  and  $s_2^2$  are the two sample variances

$n_1$  and  $n_2$  are the sample sizes

$t_1$  and  $t_2$  are the 0.975 quantiles of the Student t-distribution with  $n_1 - 1$  and  $n_2 - 1$  degrees of freedom, respectively

$\chi_{11}^2$  ( $\chi_{12}^2$ ) and  $\chi_{21}^2$  ( $\chi_{22}^2$ ) are the 0.025 (0.975) quantiles of the chi-squared distribution with  $n_1 - 1$  and  $n_2 - 1$  degrees of freedom, respectively.

Ride suggests that if both  $CD_1$  and  $CD_2$  are 1.5 or greater the two populations warrant subspecific separation, if neither reaches 1.5 it is probable that the populations are not subspecifically distinct, while if  $CD_1$  is less than 1.5 and  $CD_2$  1.5 or more further data is necessary to reach a conclusion.

The above procedure is invalid for two reasons:

- (i) Since the higher the value of the coefficient of difference, the more distinct are the two populations, a one sided confidence interval of the form  $(CD_1, \infty)$  is required. In statistical terms, one is testing the null hypothesis

$$H_0: CD < 1.5$$

against the one-sided alternative

$$H_1: CD \geq 1.5,$$

and the larger the value of the calculated coefficient of difference, the greater the evidence in favour of  $H_1$ . In practice, it is not possible to test  $H_0$  against  $H_1$ , since  $H_0$  is not a simple hypothesis (including as it does a whole range of values of CD). Therefore one replaces this range of values by the largest allowable value of CD which is not sufficient to warrant subspecific separation, namely 1.5. We then test

$$H_0: CD = 1.5$$

against

$$H_1: CD > 1.5,$$

and high values of the sample coefficient of difference, i.e. those in an interval of the form  $(CD_1, \infty)$ , are significant.

- (ii) In obtaining the upper and lower points  $CD_2$  and  $CD_1$ , Ride has stated that the lower point of the confidence interval for the ratio  $(\mu_2 - \mu_1) / (\sigma_1 + \sigma_2)$  is obtained by combining the lower point for the numerator with the upper point for the denominator (and similarly for the upper point of the confidence interval). This procedure would be valid if  $\bar{x}_2 - \bar{x}_1$  and  $s_1 + s_2$  were perfectly

negatively correlated with each other. To obtain a confidence interval for  $(\mu_2 - \mu_1) / (\sigma_1 + \sigma_2)$  one must obtain the distribution of the ratio  $(\bar{x}_2 - \bar{x}_1) / (s_1 + s_2)$ , considering the joint distribution of  $\bar{x}_2 - \bar{x}_1$  and  $s_1 + s_2$ . As a result, Ride obtains confidence intervals which are much wider than they should be.

We now give a valid statistical procedure for testing for subspecies.

### Estimation of Coefficient of Difference and Statistical Inference

If  $\sigma_1 \neq \sigma_2$ , it is difficult to relate the CD value to the proportion of overlap. Moreover, unless  $\sigma_1 = \sigma_2$ , it is not possible to obtain exact statistical procedures for making inferences concerning the value of CD. Since in practice it is difficult to reject the hypothesis that  $\sigma_1 = \sigma_2$  (using an F-test based on  $s_1/s_2$ , values vastly different from unity being significant) we will proceed on the basis that the population variances are equal.

Assuming that  $\sigma_1 = \sigma_2$ , and given samples  $(x_{1i}, i = 1, 2, \dots, n_1)$ ,  $(x_{2i}, i = 1, 2, \dots, n_2)$  of  $n_1$  values of  $X_1$  and  $n_2$  values of  $X_2$ , the usual estimator of CD is

$$(10) \quad \hat{CD} = \frac{\bar{x}_2 - \bar{x}_1}{2s},$$

where  $\bar{x}_1$  and  $\bar{x}_2$  are the sample means and  $s$  is the (pooled) sample standard deviation, i.e.

$$s^2 = \{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2\} / (n_1 + n_2 - 2),$$

$$(11) =$$

$$\frac{1}{n_1 + n_2 - 2} \left\{ \sum_{i=1}^{n_1} (x_{1i} - \bar{x}_1)^2 + \sum_{i=1}^{n_2} (x_{2i} - \bar{x}_2)^2 \right\}.$$

Now it follows from (10) after some manipulations, that

$$\hat{CD} = \phi_1 - \alpha \left\{ \frac{n_1 + n_2}{4n_1 n_2} + \frac{(\hat{CD})^2}{2(n_1 + n_2 - 2)} \right\}^{1/2}.$$

$$\frac{\bar{x}_2 - \bar{x}_1 - (\mu_2 - \mu_1)}{(\sigma^2/n_1 + \sigma^2/n_2)^{1/2}} + \left( \frac{4n_1 n_2}{n_1 + n_2} \right)^{1/2} \frac{\mu_2 - \mu_1}{2\sigma} \\ \frac{\{ (n_1 + n_2 - 2) s^2 / \sigma^2 \}^{1/2}}{(12) =}$$

$$\frac{1}{\beta} (n_1 + n_2 - 2)^{1/2} \cdot \frac{X + \beta(CD)}{X n_1 + n_2 - 2} = \frac{1}{\beta} t\{\beta(CD)\},$$

where  $X$  has a standardized normal distribution,  $X^2 n_1 + n_2 - 2$  has an independent chi-squared distribution with  $n_1 + n_2 - 2$  degrees of freedom, and  $\beta = \sqrt{4n_1 n_2 / (n_1 + n_2)}$ . Thus  $\beta \hat{CD}$  has a non-central t-distribution (see, for example, Keeping, 1962, p. 190) with  $n_1 + n_2 - 2$  degrees of freedom and noncentrality parameter  $\beta(CD)$ . Using standard tables of the non-central t-distribution (see, for example, Resnikoff and Lieberman, 1957) one can now obtain a confi-



dence interval for CD. The procedure is as follows.

- (i) Calculate  $\hat{\beta}CD$  from the sample.
- (ii) Determine, from the tables, the value of the non-centrality parameter  $\beta(CD_1)$ , say such that  $\Pr\{t\{\beta(CD_1)\} < \hat{\beta}CD\} = 1 - \alpha$ .
- (iii) The  $(1 - \alpha)\%$  confidence interval for CD is then  $(CD_1, \infty)$ . (If  $\alpha = 0.05$ , a 95% confidence interval will be obtained.)

The procedure is now to accept subspecific classification if  $CD_1$  is greater than 1.5 (say), with  $(1 - \alpha)\%$  certainty of being correct.

#### Large Sample Theory

If  $n_1$  and  $n_2$  are moderately large one can obtain an approximate confidence interval for CD without use of tables. This is based on the fact that  $\hat{CD}$ , suitably scaled, has a limiting standardized normal distribution as  $n_1$  and  $n_2$  tend to infinity. Using the law of large numbers,  $\bar{X}_2 - \bar{X}_1 \rightarrow \mu_2 - \mu_1$  and  $s \rightarrow \sigma$  as  $n_1$  and  $n_2 \rightarrow \infty$ , so that

$$E[\hat{CD}] \rightarrow \frac{\mu_2 - \mu_1}{2\sigma} = CD$$

as  $n_1, n_2 \rightarrow \infty$ . Similarly it is possible to show that

$$\text{var}[\hat{CD}] \sim \frac{n_1 + n_2}{4n_1 n_2} + \frac{(CD)^2}{2(n_1 + n_2 - 2)},$$

as  $n_1, n_2 \rightarrow \infty$ . Since  $\{\hat{CD} - CD\} / \{\text{var}[\hat{CD}]\}^{1/2}$  is asymptotically standardized normally distributed, an approximate  $(1 - \alpha)\%$  confidence interval for CD is  $(CD_1^*, \infty)$ , where

$$(13) \quad CD_1^* =$$

$$\hat{CD} - \left\{ \frac{(n_1 + n_2 - 2)(n_1 + n_2)}{4n_1 n_2} \right\}^{1/2}$$

and  $\phi_{1-\alpha}$  is the  $1 - \alpha$  quantile of the standardized normal distribution. In particular a 95% confidence interval is given by  $\phi_{0.95} = 1.64$ .

An indication of the exactness of the asymptotic approximation (13) is given by comparing  $CD_1^*$  and  $CD_1$  for moderate values of  $n_1$  and  $n_2$ . These values were checked and found to be in close agreement for the data analysed in Table 1 in the preceding article. For example, for the characteristic  $M_1$ , in the case of the two populations "Modern *Thylacinus cynocephalus*" and "Eucla Division Fossil *Thylacinus*", it was found that at the 95% level  $n_1 = 39$ ,  $n_2 = 7$ ,  $\hat{CD} = 1.16$ ,  $CD_1 = 0.76$ ,  $CD_1^* = 0.78$ .

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## Obituary

### Eric Mervyn Watson 1903-1971

An Honorary Member and former President of the Royal Society of Western Australia, Dr. Eric Mervyn Watson, died at Augusta on September 7th, 1971 at the comparatively early age of 68. In addition to his period of office as President (1943-1944), Dr. Watson was Treasurer of the Society for ten years, and a member of the Council from 1936 to 1952.

Entering the University of Western Australia in 1922 from Perth Modern School, Eric Watson majored in Chemistry, completing his first degree in 1924 and an Honours degree in 1925. He was a student under Professor N. T. M. Wilsmore, and one of many graduates of that era who reached the top levels of the profession. After several positions as an industrial chemist, and temporary lectureships at the University of Adelaide and the University of Western Australia, he joined the teaching staff of Perth Technical College in 1929, and spent the remainder of his working life in that institution. Initially appointed an Assistant Lecturer, he rose through the various grades of Lecturer to be head of the Chemistry Department in 1946. During this time he became recognized as an authority on the training of chemists and pharmacists, and was honoured by election to Fellowships of both the Royal Australian Chemical Institute, and the Pharmaceutical Society of Victoria.

In 1930, soon after his appointment at Perth Technical College, Eric Watson was awarded a Hackett Studentship, which enabled him to study at Imperial College in the University of London for a degree of Doctor of Philosophy in the field of organic chemistry. Returning to the College in 1933, he began using the limited research facilities at his disposal to make studies in the chemistry of some Western Australian plants, in particular the eucalypts, and published the results in the *Journal of the Royal Society of Western Australia*. Although World War II ended this work the knowledge gained was valuable when he became a member of the Western Australian Drug Panel, which was set up to seek alternative sources for a number of pharmaceutical preparations which had been cut off because of hostilities. He was also active in Air Raid Precaution work, lecturing in chemical defence.

From the time he returned from London in 1933, Dr. Watson became increasingly involved in the teaching of Pharmacy students. Pharma-

cology had become a more exact science, and many of the older drugs in the form of plant extracts were being dropped in favour of pure organic chemicals. Pharmacists required a better knowledge of organic chemistry and biochemistry, and Dr. Watson was called on to supply it. He became keenly interested in raising the standard of education in pharmacy, but was also closely involved in establishing various Associateship courses in chemistry at Perth Technical College as qualifications for technologists in industry. In the later years of his career he was responsible for the initial planning of the Chemistry Department at the new Institute of Technology at Bentley.

To the staff of the College who knew him well, Eric Watson was recognized as an outstanding personality. His scholarship, his skill in organising, his ability as a lecturer, and his general capacity for getting things done, earned the respect of all his colleagues. He had little time for educational theorists, and none at all for "red tape" and other administrative tangles.

His students found him a teacher whose material was always well prepared, and whose chemical knowledge was encyclopaedic. He had the reputation of setting a very high standard, but whether or not this was so, at least his students could hold their own in the outside world, and many of them rose to high positions in their professions.

A few years after becoming head of the Chemistry Department Dr. Watson suffered a severe heart attack, and although he made a good recovery, care had to be observed in the years that followed. This involved curtailment of many of his activities, including membership of the Royal Society Council. He sought no further promotion in the College, and retired in 1963 in his 60th year. An active sportsman in his early years, he retained a strong interest in fishing, and spent the last eight years of his life in retirement at Augusta where he could indulge in his hobby. Even then he could not completely drop his active intellectual pursuits, and with his wife was instrumental in setting up a branch of the Western Australian Historical Society at Augusta, of which he was the first President.

The sympathy of all members of the Royal Society goes to his widow, Mrs. Rose Watson, and to his son and daughter.









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